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VERS UN AMÉNAGEMENT DES FORÊTS COMPLEXES: DÉCRIRE ET MESURER LA COMPLEXITÉ DES FORÊTS

THÈSE PRÉSENTÉE COMME EXIGENCE PARTIELLE

DU DOCTORAT EN BIOLOGIE

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Cette thèse est présentée sous la forme de trois articles scientifiques rédigés en anglais. Au moment du dépôt de cette thèse, le premier chapitre est en cours de préparation pour sa soumission à la *Revue canadienne de la recherche forestière*. Le chapitre 3 est présenté à un atelier sur l'aménagement multicohorte en forêt boréale ('Boreal Multi-cohort Forest Management Workshop', Cochrane, Ontario) en vue d'une publication dans une édition spéciale de *Forestry Chronicle* dans le numéro de juillet/août. Le chapitre 2 sera soumis prochainement à *Ecography*.

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ANOVA	Analysis of Variance
DBH	Diameter at Breast Height
DHP	Diamètre à hauteur de poitrine
HSV	Hue Saturation Value : Méthode de codage des couleurs dans les photographies numériques
IDH	Intermediate Disturbance Hypothesis (Hypothèse de la perturbation intermédiaire) (Connell, 1978 ; Denslow, 1985)
LIDAR	Light Detection And Ranging (télédétection par laser)
MIG	Mean Information Gain (Andrienko, Brilliantov and Kurths, 2000 ; Proulx and Parrott, 2008)
MMI	Mean Mutual Information (Andrienko, Brilliantov and Kurths, 2000 ; Proulx and Parrott, 2008)
NDVI	Normalized Difference Vegetation Index
PC	Partial Cut
PCA	Principal Component Analysis
RDA	Redundancy analysis
SCI	Structural Complexity Index (Zenner and Hibbs, 2000)
TRIADE	Projet pilote de zonage pour l'aménagement écosystémique en Mauricie (Québec)

RÉSUMÉ

Le changement de paradigme qui a actuellement lieu en foresterie constitue une formidable opportunité pour l'introduction de nouvelles idées et concepts pour la compréhension et l'aménagement forestier. Notamment, le développement de l'aménagement écosystémique, qui implique la compréhension des systèmes et l'adaptabilité de l'aménagement, entraîne un ensemble de nouveaux questionnements et le développement d'un ensemble d'outils permettant de quantifier leurs différents impacts.

Les indicateurs des effets de l'exploitation sur les systèmes forestiers sont généralement basés sur la diversité spécifique et la structure de la population d'arbres. Ces métriques, tout en étant de bons indicateurs de la sévérité des perturbations, sont toutefois insuffisantes pour rendre compte de leur impact sur la structure et le fonctionnement du système dans son ensemble.

D'autre part, les travaux touchant à la compréhension des systèmes complexes se développent de plus en plus en écologie. Ces systèmes sont décrits comme des systèmes adaptatifs, caractérisés par des dynamiques non-linéaires, émergeants des interactions entre de multiples agents. Ces systèmes, et l'imprédictibilité de leur dynamique, ont motivé le développement d'une approche intégrative permettant de représenter leurs propriétés et patrons émergents.

L'introduction des théories et méthodes issues de la complexité en écologie forestière permettrait d'approcher les systèmes de manière plus intégrative et notamment d'exploiter mieux l'information contenue dans les patrons spatiaux.

Le travail de thèse présenté ici a pour objectif général de contribuer à l'introduction de ces méthodes dérivées de l'étude des systèmes complexes. Pour cela, nous avons exploré deux approches bien distinctes mais complémentaires des systèmes complexes.

Tout d'abords, nous proposons d'exploiter la théorie des réseaux en écologie de manière à intégrer une compréhension des forêts au travers des interactions qui les structurent (Chapitre 1). Cette approche pourrait de surcroît être utilisable pour l'aménagement forestier puisqu'elle permet d'identifier les éléments et processus les

plus important pour l'ensemble du système et donc de développer des méthodes adaptées à leur conservation. D'autre part, l'étude de ce type de réseau d'interactions se base sur la compréhension des déterminants des patrons de distributions des structures forestières. Cette approche se situe directement dans la lignée des méthodes en écologie du paysage, tout en intégrant encore plus les nouveaux outils de mesure de patrons (photographie numérique, LIDAR, satellite) et donc l'étude des patrons formés par les systèmes forestiers mais détachés de l'inventaire des individus.

D'autre part, mais toujours dans l'objectif de développer l'exploitation de l'information contenue dans les patrons spatiaux, nous avons mis en pratique une méthode de mesure directe de la complexité des patrons dans les photographies numériques (chapitres 2 et 3). Cette méthode permet de quantifier la complexité des patrons émergents des communautés forestières, sans avoir besoin d'en inventorier tous les individus.

Nous avons particulièrement vérifié si le lien entre complexité et hétérogénéité structurelle ou diversité spécifique qui est communément fait dans la littérature est réellement valide, et donc si l'inventaire de l'hétérogénéité et de la diversité des structures pouvait réellement servir d'indicateur de complexité (chapitre 2). Nos conclusions indiquent que l'hétérogénéité et la complexité sont en fait négativement reliées. En réalité, les systèmes les plus hétérogènes tendent à former des patrons réguliers puisque la végétation remplie tout l'espace disponible. Nous avons également noté grâce à ce travail que la mesure directe des patrons dans les photographies numériques intègre également les patrons formés par lumière. Cet aspect de notre mesure de complexité nous parait extrêmement intéressant dans le cadre du développement de méthodes pour le suivi de l'aménagement écosystémique.

Justement, notre cadre de travail au sein du projet TRIADE nous a également permis de tester notre méthode dans un contexte opérationnel de coupes écosystémiques (chapitre 3). Différentes intensités de coupes partielles sont ainsi comparées à des forêts secondaires et matures pour vérifier si ces méthodes de coupe sont propres à maintenir ou promouvoir la complexité des systèmes perturbés. D'après nos résultats, il apparaît que les coupes partielles sont finalement plus complexes que les forêts fermées. En fait, la relation entre l'ouverture de la canopée (utilisée comme indicateur de perturbation) et la complexité des patrons démontre que 'l'hypothèse des perturbations intermédiaires' ('Intermediate Disturbance Hypothesis') serait applicable pour la prédiction des patrons de complexité : les systèmes les moins perturbés et les systèmes les plus perturbés sont plus réguliers que ceux soumis à des perturbations modérées.

Mots Clefs : Complexité, Patrons spatiaux, Réseaux, Forêt boréale mixte, Mean Information Gain, Aménagement écosystémique, Structure, Diversité, Hétérogénéité.

Keywords: Complexity, Spatial patterns, Networks, Mixed-wood boreal forest, Mean Information Gain, Ecosystem management, Structure, Diversity, Heterogeneity.

INTRODUCTION

0.1 Complexité et forêts

De plus en plus, les systèmes écologiques sont considérés comme des systèmes complexes. Ces systèmes ne sont pas définis par leur composition ou leur identité mais plutôt par leur imprédictibilité. La dynamique des systèmes complexes est typiquement définie à la frontière entre déterminisme et stochasticité. Leur dynamique et les patrons spatiaux qui en résultent sont donc typiquement déterministes, mais marqués par des événements imprévisibles.

L'existence de mécanismes d'autorégulation dans le système et l'entrelacement de structures ayant des effets à plusieurs niveaux hiérarchique peuvent être considérés comme des indicateurs (ou des inducteurs) de complexité. L'addition de ces attributs peut provoquer l'apparition de propriétés émergentes imprédictibles à l'échelles des éléments individuels. Ces propriétés émergentes peuvent contribuer à leur tour à la dynamique des systèmes et ainsi amplifier l'imprédictibilité des dynamique des systèmes (Stone and Ezrati, 1996 ; Heylighen, 1997 ; Levin, 1998 ; Parrott, 2002 ; Anand and Tucker, 2003 ; Cadenasso, Pickett and Grove, 2006). De manière plus succinct, mais peut être moins quantifiable, la complexité peut être considérée comme une métrique de la multiplicité des interactions entre éléments et échelles (Ascher, 2001).

L'étude des systèmes complexes a été motivée par la volonté de compréhension des systèmes naturels et sociaux imprédictibles mais présentant un intérêt à être prédits (systèmes climatiques, écologiques) ou gérés (hydrologie, urbanisme). Le seul

point commun apparent de ces systèmes est leur imprédictibilité à certaines échelles malgré les comportements déterministes de leurs composantes. Les systèmes climatiques par exemples sont composés de molécules de gaz différents répondant toutes à un ensemble de lois simples, mais à plus grande échelle, la dynamique des masses d'air est difficilement prévisible en utilisant seulement ces lois (Goldenfeld and Kadanoff, 1999). Ainsi, bien que la composition du système ne change pas, la construction des modèles de prédiction peut être radicalement différente en fonction de l'événement à prédire. Par analogie, les systèmes végétaux ne peuvent pas être schématisés de la même manière selon qu'on s'intéresse à un individu, aux relations entre un petit nombre d'individus, ou à un peuplement entier. Si la physiologie d'un individu est assez bien décrite par des modèles réductionnistes, les dynamiques des peuplements ou des paysages sont mieux prédites par des modèles intégrant des composantes empiriques –souvent basés sur l'expérience de la phytosociologie– ou statistiques (modèles neutres ou nuls) (Hubbell, 2001).

De nombreux travaux depuis le début du 20^{e} siècle confrontent déterminisme environnemental et stochasticité d'assemblages compatibles pour la formation des communautés et l'explication des mécanismes émergents (Clements, 1916 ; Gleason, 1917). Dans un autre contexte et avec un point de vue orienté vers la compréhension holistique des systèmes et leur conservation, la métaphore du super-organisme qui fut reprise, développée, contestée et modifiée plus tard par différents auteurs (Lovelock and Margulis, 1974 ; Levin, 2005) est également apparue pour expliquer les phénomènes de successions, de rétroaction et de stabilité relative des systèmes face aux perturbations. Cette théorie comparait déjà les mécanismes d'adaptation des peuplements à l'évolution des espèces. Cependant, le principe des successions et de la coexistence des espèces sont actuellement expliqués comme résultant des interactions positives et négatives en relation avec l'environnement abiotique, et donc par des mécanismes agissant strictement à l'échelle des individus (Grime, 1974 ; Tilman, 1988). Néanmoins, l'idée d'une échelle d'organisation plus grande que les individus

est ancienne et revient régulièrement dans les débats en écologie des communautés (Clements, 1916 ; Lovelock and Margulis, 1974 ; Holling, 1992).

Dans le but d'intégrer plusieurs dimensions (spatiales, temporelles et hiérarchiques) dans l'étude des écosystèmes et d'envisager leur fonctionnement en utilisant les approches issues d'autres sciences Colwell (1998) a créé le néologisme 'biocomplexité' (de biologie et complexité) pour caractériser les interactions complexes entre sciences, individus et méthodes pour l'étude de systèmes eux-mêmes complexes (Michener *et al.*, 2001 ; Pickett, Cadenasso and Grove, 2005). Cette notion avait autant pour objectif de considérer les systèmes de manière holistique que de promouvoir les échanges entre disciplines. Depuis, les interactions entre domaines de recherche se sont effectivement développées permettant la création d'outils statistiques et de modélisation adaptés. Certains modèles issus des sciences physiques sont notamment testés en écologie (automates cellulaires...). L'approche des patrons abstraits de fréquence d'événements ou certaines relations entre descripteurs des systèmes ont notamment été revisités à la lumière des systèmes complexes. Ainsi, plusieurs travaux ont montré que les densités de certains groupes d'espèces, les fréquences des feux et la relation entre taille et croissance des individus peuvent correspondre à des lois de puissance ou des relations exponentielles (Perry, 1995 ; Jorgensen, Mejer and Nielsen, 1998 ; Enquist and Niklas, 2001 ; Niklas and Enquist, 2001). Ces relations démontrant le déterminisme non-linéaire de ces relations, et surtout un ensemble de propriétés utilisables en modélisation (invariance de la relation à l'échelle). Cependant, ces propriétés émergentes ont été vérifiées à des échelles spécifiques et leur soumission à une loi de puissance est rarement confirmée à leurs asymptotes (dans les valeurs extrêmes des gradients). En addition, certains indices originellement créés pour l'étude des fréquences d'événements dans les systèmes chaotiques sont à présent utilisées pour la caractérisation de série temporelles issues de systèmes écologiques complexes (Symonides, Silvertown and Andreasen, 1986 ; Bak, Tang and Wiesenfeld, 1988 ; Stone and Ezrati, 1996). Dans

le cadre des études liées au chaos, certaines variations annuelles supposées cycliques ou à l'inverse aléatoire ont montré des dynamiques plus 'complexes'. Les quantités de graines produites annuellement par les semenciers sont supposées être liées au climat et au fitness des individus avec une forte stochasticité associée (autrement dit du 'bruit'), mais des travaux axés sur l'étude des systèmes chaotiques ont montré que ces quantités peuvent varier de façon quasi-chaotique d'une année à l'autre, traduisant une forte sensibilité à d'infimes variations des conditions initiales (Symonides, Silvertown and Andreasen, 1986 ; Stone and Ezrati, 1996). A l'inverse des processus et relations exponentielles ou suivant des lois de puissance, ces dynamiques quasi-chaotiques ne permettent que peu de certitude dans les prédictions. Ces conclusions remettent en question la nature du 'bruit' dans les données biologiques, et donc l'utilisation de modèles strictement déterministes pour leur description (Wu and Loucks, 1995 ; Pascual and Levin, 1999).

Deux facettes de l'imprédictibilité des systèmes écologiques sont ici illustrées, d'une part des relations imprévisibles parce qu'inattendues (les propriétés émergentes), et d'autre part l'imprédictibilité de dynamiques pourtant issues des relations supposées déterministes au niveau de l'individu (dynamiques quasi-chaotiques). Ces différents exemples d'imprédictibilité sont la conséquence de la multiplicité des éléments étudiés et de leurs interconnections spatiales, écologiques ou évolutives (Noss, 1990 ; Holling, 1992 ; Heylighen, 1996). Bien que plusieurs travaux tentent de réduire l'imprédictibilité des dynamiques des systèmes écologiques complexes ou de schématiser leur fonctionnement, l'étude de ces systèmes en écologie n'en est encore qu'à la phase descriptive.

Pour palier à ce manque de certitude dans la prédiction des dynamiques des systèmes écologiques, la gestion des systèmes forestiers se doit d'impliquer des outils qui permettent d'intégrer l'imprédictibilité spatiale et temporelle des écosystèmes forestiers. Les objectifs de production devraient être flexibles et s'adapter aux évènements et aux réponses des écosystèmes. Cependant, du point de vue des

gestionnaires, les milieux forestiers sont encore considérés comme déterministes et sécables en unités indépendantes dans le temps et l'espace et les variations dans la dynamique des systèmes sont souvent assimilées à du bruit dans les données ou à l'influence d'éléments extérieures aux systèmes. Les limites spatiales et temporelles qui sont imposées par la gestion humaine sont donc probablement à reconsidérer pour améliorer la réactivité des plans d'aménagement et permettre une gestion intégrant différentes échelles.

0.2 La gestion écosystémique

Sous la pression de différents groupes sociaux, les pratiques de gestion se dirigent aujourd'hui vers des traitements plus hétérogènes qui offrent plus de variabilité aux milieux. Cette évolution marque vraisemblablement un premier pas vers la complexification des pratiques forestières, cependant ce changement de méthode a principalement pour effet d'améliorer la physionomie des forêts, c'est-à-dire leur apparence visuelle, et de ce fait l'acceptabilité sociale des traitements appliqués. Cette logique repose moins sur des principes écologiques que sur les attentes éthico-esthétiques des groupes d'intérêts impliqués dans la gestion du paysage (populations locales, villégiateurs, randonneurs, environnementalistes, chasseurs, ...) (Kimmins, 2003). L'aménagement qui est pratiqué dans ce but est souvent lié à des interventions lourdes et répétées d'entretien des peuplements afin de garantir les objectifs de l'exploitant. Même si l'effet à court terme sur la structure forestière semble 'naturel' pour le publique, les méthodes employées modifient le milieu à long terme et lui font perdre de la variabilité (Solomon and Gove, 1999). L'hétérogénéité structurelle des peuplements forestiers pourrait n'être conservée qu'à très petite échelle (microsite ou bouquet d'arbre), mais à une échelle plus large (parcelle, paysage), l'échantillon de structures présélectionnés par le gestionnaire pourrait limiter l'hétérogénéité (représentation des classes d'âges et des espèces désirables, quantité et répartition du bois mort,...).

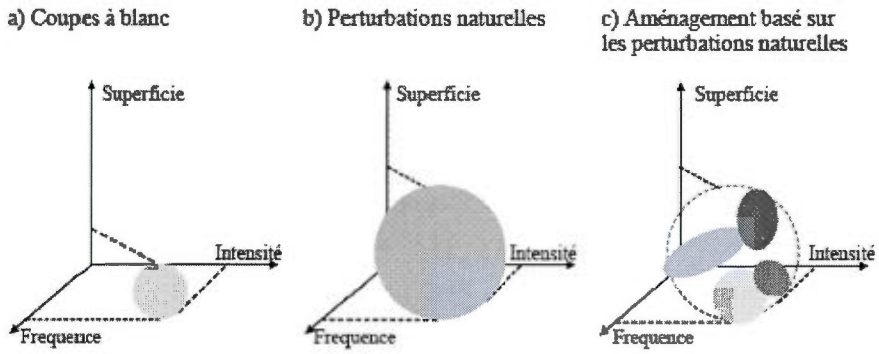

Figure 0.1 Visualisation des perturbations selon leur intensité, fréquence et surface. a) Coupes à blanc, b) Perturbations naturelles; c) Spectre de perturbations désirable en aménagement écosystémique basé sur les perturbations naturelles (inspiré de Haeussler and Kneeshaw, 2003).

D'autres méthodes de récolte et d'aménagement rassemblées sous l'appellation d'aménagement écosystémique visent à gérer les milieux en tenant compte de leur écologie ou plutôt en considérant leur variabilité naturelle. Le but général de ces méthodes est de promouvoir l'autorégulation et la résilience des systèmes en conservant les possibilités d'adaptation du milieu (Messier and Kneeshaw, 1999 ; Ascher, 2001). L'aménagement par émulation des perturbations naturelles (natural disturbance-based management), qui consiste à mimer les effets des perturbations naturelles pour profiter des mécanismes naturels de restauration est un exemple de cette philosophie de gestion (Drever *et al.*, 2006). Selon les perturbations endogènes au système (insectes, feux, chablis), l'intensité, la fréquence et l'aire des activités sylvicoles sont ajustées pour se rapprocher des caractéristiques des perturbations naturelles (Figure 0.1). Cela dit, certaines caractéristiques de ces perturbations sont impossibles à reproduire ou à atténuer : l'enrichissement du sol en carbone après les feux n'est pas imité, l'impact spécifique des engins de coupe et de débardage n'est atténué que partiellement et les surfaces coupées ne peuvent pas être étendues au delà des lots attribués à l'exploitant et de certaines contraintes réglementaires (conservation des bandes riveraines, proximité des habitations...).

Les interventions d'aménagement écosystémique tendent souvent à conserver une plus grande proportion du couvert forestier que les interventions sylvicoles traditionnelles. La conservation d'un couvert d'arbres résiduels contribue à la fois à la conservation de la stratification verticale et de la complexité de la structure horizontale du peuplement. De plus, la rétention de structures variées (arbres matures, taillis, arbres morts, jeunes individus...) permet d'accélérer la restauration des milieux en servant de puits de recolonisation et de corridor entre milieux fermés. Le couvert résiduel permet aussi de limiter la modification des propriétés abiotiques du site avec notamment un impact positif sur la germination et la recolonisation (Franklin *et al.*, 2002 ; Ries *et al.*, 2004 ; Drever *et al.*, 2006). Bien que la qualité des lits de germination reste le facteur prédominant pour la germination (Calogeropoulos et al., 2004), les conditions d'ouverture de la canopée influent également sur l'implantation des espèces forestières de fin de succession (McLaren and Janke, 1996 ; Claveau *et al.*, 2002 ; Aubin, Messier and Kneeshaw, 2005 ; Claveau, Messier and Comeau, 2005). L'humidité des lits de germination qui est conservée par l'ombrage de la canopée et les conditions d'éclairage des strates basses sont notamment impliqués dans les modification des conditions de germination après les coupe (Duchesneau and Morin, 1999). L'aménagement écosystémique en faisant varier les surfaces, les formes des ouvertures et la structure des peuplements exploités (répartition des ouvertures et des éléments résiduels) vise finalement à créer un éventail de conditions environnementales propres à favoriser l'émergence de cohortes d'espèces variées puisque adaptées à ces différents milieux. En augmentant les potentialités d'assemblages dans les peuplements, on vise à augmenter l'adaptabilité des systèmes forestiers et donc à garantir leur résilience (Grumbine, 1994 ; Wu and Loucks, 1995 ; Levin, 2005). Ces méthodes d'aménagement ont aussi l'avantage de conserver les structures non arborées (sous-bois et sol, microtopographie) sous les arbres résiduels. De cette manière, la restauration des propriétés des lits de germination profite de la conservation des banques de graines et des populations mycorhiziennes. Les mycorhizes interagissent localement avec les végétaux

vasculaires et contribuent aux échanges latéraux d'eau et de nutriments entre eux. Ces échanges sont assez importants dans le système pour accélérer la recolonisation de milieux ouverts (Perry, 1995 ; Simard and Durall, 2004).

Cependant, puisque l'aménagement écosystémique vise à la durabilité des pratiques autant du point de vue environnemental qu'économique ou social (i.e. : politique), la mise en oeuvre des méthodes d'aménagement écosystémique peut différer significativement d'un pays à l'autre et selon les priorités des gestionnaires. Ainsi, dans les pays producteurs de bois (pays scandinaves, Canada, USA...) la priorité est à la conservation des rendements de production pour le futur, mais les pressions sociales contraignent les exploitants à mettre en place des pratiques plus acceptable par le public impliqué, notamment en termes de conservation et d'accès aux systèmes forestiers et aux ressources non ligneuses. Les entrepreneurs sylvicoles sont donc contraints de conserver certaines structures ciblées par les autorités (bandes riveraines, lisières...). Dans les pays touchés par des catastrophes naturelles (feux catastrophiques, inondations, érosion) la priorité est à la conservation des forêts pour leurs capacités de protection (rétention des sols, protection des bassins versants...). Ces contraintes impliquent des mesures de protections à plus grande échelle qui sont parfois même en désaccord avec les objectifs de conservations (par exemple, les corridors anti-feu dans les forêts du sud de la France) (Dekker *et al.*, 2007). Les différentes pratiques d'aménagement écosystémique se différencient notamment par les éléments du système forestier inclus dans les objectifs d'aménagement, le développement du sous-bois par exemple est plutôt valorisé dans les cas d'une protection des sols et des nappes phréatiques. Un objectif pour les futures gestionnaires serait ainsi d'inclure un maximum de valeurs forestières (diversité, protection, ressources) dans les plans de gestion afin de les aménager en pleine connaissance des différents enjeux. La définition opérationnelle des milieux forestiers doit ainsi évoluer et intégrer ces différentes valeurs. Les processus non linéaires de vieillissement des peuplements tels que le remplacement d'un cortège d'espèces

rudérales par un assemblage de milieux fermés pourront être intégrés aux modèles de prédiction (Holling, 1992). Cela permettrait notamment de limiter les erreurs de prédiction de possibilité forestière qui ne tient actuellement pas compte (notamment au Québec) de la répartition des peuplements dans l'espace ni des variations du cortège végétal entre les moments de l'estimation et de la récolte (Ruel *et al.*, 1998). D'autre part, la compréhension des processus de rétroaction et des propriétés émergentes du système permettra éventuellement leur manipulation dans le cadre des pratiques de gestion afin de minimiser la fréquence et l'intensité des interventions sylvicoles (Perry, 1995). Ces améliorations des pratiques sylvicoles passent par une période d'évaluation et d'expérimentation sur le terrain.

0.3 Indicateurs d'intégrité écologique et complexité

Pour évaluer les impacts des pratiques de récolte et vérifier que les objectifs de restauration des milieux après coupe sont atteints, des indicateurs sont nécessaires. Plusieurs types d'indicateurs d'intégrité forestière ou de qualité des systèmes sont déjà utilisés en conservation et en foresterie. Les indices utilisés en conservation sont souvent centrés sur la diversité en espèce ou la présence de groupes d'espèces particulières, alors que les indices utilisés par les forestiers sont plutôt axés sur la strate arborée et le volume de matière ligneuse disponible. Ces indices ont pour objectif de schématiser le milieu forestier en quantifiant certains services rendus (ici la diversité ou la productivité). Souvent, ces indices sont évalués par comparaison avec des milieux anciens pour mesurer la distance entre milieu 'naturel' et milieu géré et donc l'intégrité écologique (ou la naturalité) du milieu (Frego, 2007). Comme l'aménagement forestier influe directement sur la structure des habitats (Franklin *et al.*, 2002 ; McElhinny *et al.*, 2005), certains indices structurels reflétant l'impact des perturbations anthropiques sont confrontés aux indices de diversité. Les effets de l'hétérogénéité des peuplements et des paysages ont été étudiés sur les populations animales mobiles (oiseaux et rongeurs) qui ont montré de fortes réponses aux

modifications de la couverture boisée et de la stratification (Tews *et al.*, 2004 ; Lindenmayer and Luck, 2005). Les impacts de la structure spatiale du couvert et de la répartition des éléments sur la dynamique des milieux ont également été étudiés et confirmés de nombreuses fois (McArthur, 1972 ; Ries *et al.*, 2004). Les chemins forestiers, c'est-à-dire l'ouverture de tranchées dans le couvert avec une modification des couches supérieures du sol, ont un impact sur la composition du sous-bois. Les effets des chemins se traduisent notamment par le remplacement des espèces forestières par des espèces des milieux ouverts et/ou exotiques. Un autre effet notoire est l'augmentation de l'épaisseur de la litière jusqu'à 20 cm à l'intérieur du peuplement, notamment du fait des débris de bois. Ce dernier effet des chemins implique une modification de la structure des strates forestières basses (sous-bois et sols) qui pourra modifier encore la population du sous-bois (Watkins *et al.*, 2003).

Bien que l'impact de certaines structures individuelles (grands chicots, bois mort au sol, trouées) soit bien connu, les effets de la composition en élément structurelle et de leur distribution spatiale en lien avec les effets de l'aménagement ont en revanche encore été peu étudiés. Les indices structurels les mieux connus pour le suivi de l'impact des perturbations anthropiques concernent la répartition des classes de taille (d'âge ou de diamètre) des arbres et les quantités de bois mort. Plusieurs travaux portant sur les classes de taille des arbres concluent que la structure forestière évolue en fonction de l'âge des peuplements et des perturbations qui leurs sont appliquées. Ainsi, la relation entre la densité des arbres et leur classe de diamètre (voir Figure 0.2) en forêt coupée est souvent unimodale dans les forêts gérée de manière équienne (la plupart des arbres appartiennent à la même cohorte) ou inversement proportionnelle dans les coupes partielles (le nombre d'individus est inversement proportionnel à leur taille) alors que cette relation ressemble plutôt à une loi de puissance ou à une relation logarithmique dans les forêts anciennes (courbe en J inversé) (McGee, Leopold and Nyland, 1999).

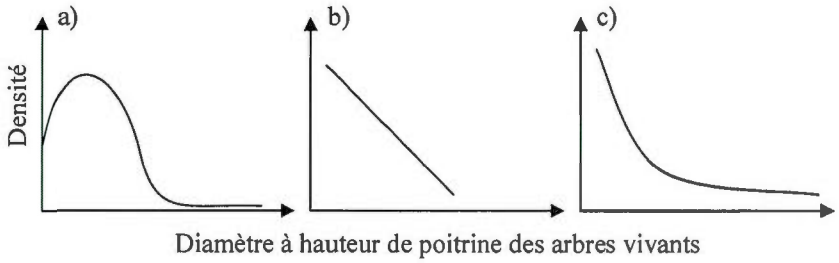

Figure 0.2 Répartition schématique des classes de diamètre des arbres vivants. a) Unimodale typique des peuplements secondaires, b) Linéaire dans les populations partiellement coupées, et c) Plutôt exponentielle négative dans les populations anciennes.

On peut également noter que l'aménagement par coupe partielle affecte autant l'âge moyen du peuplement arboré que la forme du spectre de répartition des classes d'âges (Crow *et al.*, 2002). De la même manière, plusieurs travaux montrent une baisse du nombre d'arbres morts de grand diamètre dans les milieux gérés par rapport aux forêts 'naturelles' (Marage and Lemperiere, 2005). Ces objets (grands ou vieux arbres vivants ou morts) peuvent ainsi être toujours présents dans l'inventaire des structures, mais leur proportion et donc leur impact sur le système baisse significativement.

Cependant, les études portant sur la structure des peuplements mettent souvent peu d'emphase sur le type de perturbation ou les modes de gestion appliqués et particulièrement sur les modalités temporelles et spatiales de ceux-ci. Le nombre de rotation qui ont eu lieu sur la parcelle, la fréquence des interventions ou la saison à laquelle l'exploitation a eu lieu sont aussi souvent ignorés faute d'archives (Ferguson and Elkie, 2003). Ces informations sont pourtant d'importance, puisque les legs écologiques découlant des perturbations passées s'accumulent dans le temps et influencent la structure finale des peuplements.

Les caractéristiques spatiales des perturbations (répartition des trouées dans le couvert, forme des coupes partielles) sont aussi souvent omises alors que les impacts

de la distribution spatiale et de la forme des trouées sont très variables notamment sur la pénétration de la lumière dans les peuplements (Beaudet *et al.*, 2011) ou pour la propagation des trouées (Vepakomma, St-Onge and Kneeshaw, 2011). Il est paradoxal que les études mesurant les effets des structures sur les communautés négligent autant les composantes spatiales et ne fournissent finalement que des indices en une seule dimension (densité d'arbre, DHP moyen, surface basale, hauteurs moyennes...) (Hale, Pastor and Rusterholz, 1999). Les valeurs sont souvent moyennées par peuplement (Lindenmayer, Margules and Botkin, 2000) et la seule métrique permettant d'évaluer la variabilité interne de ces éléments est souvent l'écart-type des données. L'utilisation d'indices pour évaluer un système écologique implique bien sûr de diminuer le nombre de dimensions nécessaires à la modélisation du système. Cette diminution du nombre de dimensions fait partie du processus de modélisation des systèmes et permet de concentrer l'information sur les renseignements importants et/ou manipulables. Néanmoins, pour que cette perte d'information ne soit pas préjudiciable à notre compréhension des systèmes, les dimensions à éliminer doivent être pertinentes selon le système étudié et ne devraient pas augmenter la variabilité du signal (Habeeb *et al.*, 2005). Dans une plantation homogène par exemple, la répartition des arbres dans l'espace peut être ramenée à une seule valeur de densité puisque la surface d'échantillonnage n'apporte aucune variabilité (tous les arbres étant équidistants). Dans un peuplement plus irrégulier en revanche, une deuxième dimension sera nécessaire pour tenir compte de la distribution des individus. A échelle fixe, le nombre de dimensions nécessaires pour décrire un système augmente donc avec l'hétérogénéité structurelle spatiale et fonctionnelle de celui-ci et ultimement avec l'intégration de sa dynamique (Cadenasso, Pickett and Grove, 2006) (cf. Figure 0.3).

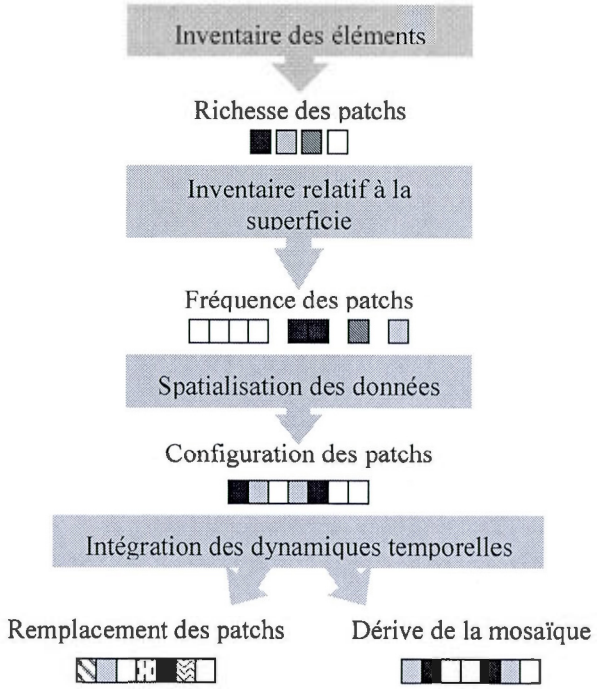

Figure 0.3 Augmentation de la complexité de la description des systèmes avec la complexité des systèmes et le nombre de dimensions dans le temps et l'espace (d'après Cadenasso, Pickett and Grove, 2006).

De plus, différents travaux sur les indicateurs de structure et d'hétérogénéité des milieux forestiers montrent que les questionnements ainsi que les descriptions des systèmes évoluent aussi selon l'échelle d'observation. La répartition des classes de diamètre et l'interprétation des patrons de succession sont par exemple connus pour varier selon la surface des aires d'échantillonnage (Frelich and Reich, 1995 ; Costanza *et al.*, 2007). Une description de la variation des résultats en fonction de l'échelle d'observation devient ainsi nécessaire. Ainsi le nombre de dimensions permettant de décrire les systèmes évolue également selon le nombre d'échelles étudiées. La complexité de la description des systèmes devrait donc augmenter en même temps que la complexité fonctionnelle, spatiale et temporelle des systèmes eux même.

En écologie forestière cependant, les dimensions d'échelles ont souvent été normalisées en 'unités' de parcelles, de peuplements ou de paysages, indifféremment de l'ampleur de la variation d'une échelle à l'autre ou des variations de la surface de ces unités en fonction de l'identité du système. Une autre approche consisterait à définir les échelles pertinentes d'observation *a posteriori* en identifiant les échelles auxquelles l'essentiel des variabilités sont causées par des relations déterministes entre objets (Pascual and Levin, 1999 ; Habeeb *et al.*, 2005) de manière à concentrer les efforts de représentation déterministe aux échelles où cette représentation est pertinente.

La structure forestière est souvent étudiée en mesurant la diversité des éléments présents dans les peuplements. Les indices de Simpson, de Shannon et l'équitabilité de la répartition des classes de taille sont ainsi utilisés pour rendre compte de la fréquence des éléments (Neumann and Starlinger, 2001 ; Tews *et al.*, 2004 ; McElhinny *et al.*, 2005). Ces indices ou modes de visualisations rendent compte de la diversité structurelle du système et donnent donc un aperçu de la variabilité des éléments à une échelle précise. De nombreux indices d'agrégation spatiale ou d'autocorrélation spatiale permettent de schématiser la distribution des éléments ou de leurs caractéristiques dans l'espace. Néanmoins ces indices ne permettent de tenir compte que d'un type d'élément ou d'une dimension à la fois (Neumann and Starlinger, 2001 ; Onaindia *et al.*, 2004 ; McElhinny *et al.*, 2005). Le calcul de ces indices est, la plupart du temps, basé sur les distances moyennes entre voisins, qui sont comparées à des répartitions régulières ou aléatoires. L'un des plus anciens de ces indices, l'indice de Pielou, permet par exemple d'évaluer la stochasticité des distances entre les positions des arbres et celles de points d'échantillonnage distribués aléatoirement ou entre plus proches voisins (Pielou, 1959 ; Neumann and Starlinger, 2001).

Les indices de diversité des éléments et ceux d'agrégation sont deux types de représentation de la structure forestière qui n'impliquent chacun qu'une dimension de

l'hétérogénéité des milieux. Ces deux types d'indices sont complémentaires mais n'ont jamais été développés pour être utilisés conjointement.

Plus récemment, Zenner et Hibbs (2000) a développé une méthode de mesure de l'hétérogénéité de la distribution des arbres tenant compte de leur répartition spatiale et de leur hauteur. Les hauteurs de chaque arbre sont mesurées dans le peuplement et des triangles sont formés grâce à une triangulation de Delaunay entre les sommets des arbres les plus proches. La somme des surfaces de ces triangles est ensuite divisée par la surface de leur projection au sol :

$$SCI = \frac{SCI^*}{A_T} \qquad \text{Eq. 0.1}$$

SCI : Structural Complexity index, SCI* : surface des triangles entre les sommets des arbres, At : surface de la projection au sol des triangles (voir Figure 0.4 ci-dessous pour une illustration de la méthode de calcul).

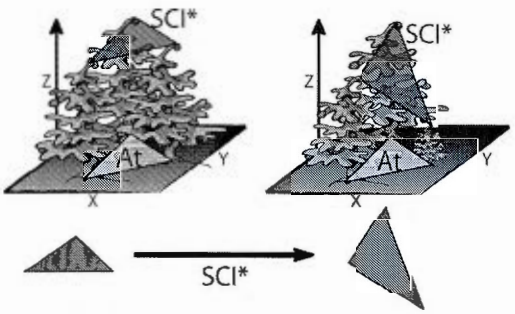

Figure 0.4 Illustration du calcule du SCI de Zenner et Hibbs (2000). SCI* représente la surface des triangles entre les sommets des arbres, At la surface des triangles projetés au sol.

Cet indice permet d'intégrer à la fois l'hétérogénéité liée aux variations des hauteurs des arbres et à leur répartition dans l'espace (donc aux voisinages de chaque individu) il rend donc compte de l'hétérogénéité spatiale de la répartition de la strate arborée en 3 dimensions. Cet indice est également adapté pour être appliqué à d'autres attributs structurels comme le diamètre des arbres (pour représenter l'hétérogénéité spatiale de la taille des arbres) (Zenner, 2000) ou la hauteur du bas de

la canopée (définissant ainsi l'hétérogénéité des strates basses de la végétation arborée).

Les approches citées précédemment sont néanmoins toutes basées sur l'utilisation des objets forestiers individuels comme base pour le calcul des indices. En forêt, ces objets forestiers sont d'ailleurs le plus souvent centrés sur les arbres. Une autre génération d'approche pour l'évaluation de l'hétérogénéité des structures et de la complexité des systèmes est basée sur la caractérisation des patrons spatiaux en eux même plutôt que sur l'inventaire de leurs composants. Ces méthodes ont été développées et sont particulièrement utilisables pour le traitement des données issues de la télédétection (Burrows *et al.*, 2002 ; Lamonaca, Corona and Barbati, 2008 ; Jaskierniak *et al.*, 2011). Par exemple, les indices dérivés du NDVI (Normalized Difference Vegetation Index) permettent d'identifier la signature des végétaux dans les images satellite et donc d'étudier leur distribution spatiale. Cet indice n'identifie pas les plantes individuelles, mais plutôt une certaine quantité d'absorption du spectre de lumière utile à la photosynthèse pour chaque pixel de l'image. Les patrons sont donc inférés à partir d'une représentation détachée des objets (Riera *et al.*, 1998 ; Roberts *et al.*, 2004). D'autre part, l'importance de la distribution, de la variabilité, de la directionnalité et de la qualité de la lumière dans les peuplements a déjà été largement étudiée (Endler, 1993 ; Gendron, Messier and Comeau, 2001 ; Beaudet, Messier and Leduc, 2004). Non seulement la distribution de la lumière en forêt est très directement influencée par la structure de la végétation et les espèces présentes (Gendron *et al.*, 2006), mais les variations de qualité (couleur, intensité, directionnalité...) et de disponibilité de la lumière sont très directement liées aux niches de régénérations (Denslow and Guzman, 2000 ; Simon, Gratzer and Sieghardt, 2011) et au fitness des populations végétales forestières. La lumière est donc à la fois un indicateur de la structure forestière (Beaudet, Messier and Leduc, 2004), mais aussi un déterminant des processus qui ont lieu et donc de la dynamique forestière (Pacala *et al.*, 1994 ; Calder, Horn and St. Clair, 2011). La distribution de la lumière

dans les forêts pourrait probablement être mieux intégrée au suivi de la structure forestière mais ne peut pas être résumée par la description de la composition structurelle (Lieffers *et al.*, 1999 ; Bellow and Nair, 2003).

De surcroît, la perception même des couleurs et des formes dans l'environnement apporte une information sur l'évolution des espèces et le fonctionnement du système. Ainsi, différents travaux montrent que la faune est influencée par l'aspect visuel de son habitat notamment par la couleur des objets pour la recherche de nourriture et le choix de ses trajets (Burns *et al.*, 2009 ; Schaefer and Kappeler, 2010).

Enfin, dans un contexte d'aménagement écosystémique où l'aspect d'acceptabilité social est prévalent, l'aspect visuel des forêts à grande échelle (habitats, paysage) devient également un indicateur important (Sheppard, 2003) et peut même devenir un déterminant pour les choix d'aménagement (Karjalainen and Tyrvainen, 2002). Différentes recherches ont notamment montré que l'apparence visuelle des habitats dans une image (photographie, images retouchées, modèles...) permettait une prise de décision plus fiable que la description des systèmes (Kim, Lee and Shelby, 2003) et que le 'ressenti' du public face à un système est souvent plus représentatif que sa connaissance des composants du système (Kohsaka and Handoh, 2006). Cependant, puisque l'origine culturelle de l'observateur a une forte influence sur les résultats des recherches sociologiques concernant l'acceptation des différents modes d'aménagement (Dramstad *et al.*, 2006 ; Kohsaka and Handoh, 2006 ; Berninger, Kneeshaw and Messier, 2009) une méthode de contrôle permettant de décrire les patrons visuels et de lier les choix visuels du publique à des critères quantifiables et aménageables est nécessaire. Notamment, les dimensions fractales des patrons observés et les discontinuités spatiales intégrées dans les images ont été utilisées de même que la composition réelle du système représenté dans les photos (Hagerhall, Purcell and Taylor, 2004 ; Dramstad *et al.*, 2006). Il apparaît que les représentations caractérisées par des patrons fractals et complexes, qui sont souvent associés à des systèmes hétérogènes et divers, ont une tendance à être préférées par le

publique (Hagerhall, Purcell and Taylor, 2004 ; Hunt and Haider, 2004 ; Dramstad *et al.*, 2006).

De nouvelles approches pour la caractérisation directe des patrons sont encore développées qui permettent notamment d'intégrer à la fois les patrons spatiaux crées par les objets représentés mais aussi les patrons spatiaux crées par la pénétration de la lumière dans les forêts. Proulx et Parrott (2008), ont notamment développé une méthode de quantification de la complexité des patrons basée sur le travail de Andrienko *et al.* (2000) permettant d'intégrer à la fois la répartition spatiale et la variabilité des éléments et de la lumière dans les patrons. Le gain moyen d'information (MIG) a notamment été utilisé sur des photographies numériques prises dans les peuplements forestiers. Les résultats ont permis de mettre en évidence la complexité des patrons émergeants de communautés de sous-bois diverses, et de démontrer un lien entre la diversité spécifique des assemblages d'espèces et la complexité des patrons (Proulx and Parrott, 2008). De plus, l'utilisation de méthodes d'échantillonnage basées sur la représentation des patrons et non pas sur l'inventaire de leurs composants (dans le cas du MIG, la photographie) permet d'envisager une normalisation des méthodes dans différents systèmes écologiques. Mathématiquement, le MIG est basé sur le calcul de la diversité des assemblages de pixels dans les photographies numériques :

$$MIG = \frac{\left[- \sum_{i=1}^{N^4} p(\chi i) \log p(\chi i) \right] - \left[- \sum_{i=1}^{N} p(\gamma i) \log p(\gamma i) \right]}{\log N^4 - \log N^1} \qquad \text{Eq. 0.2}$$

$p(\chi i)$ représente la probabilité de l'assemblage i de quatre pixels voisins dans l'image et $p(\gamma i)$ la probabilité qu'un pixel ait la valeur i indépendamment de sa position par rapport aux autres pixels. N est le nombre maximum de valeurs possible pour chaque pixel et N^4 est le nombre maximum de combinaisons de quatre valeurs de pixels. Les deux expressions entre crochets sont la diversité des assemblages de pixels (à gauche) et la diversité des pixels individuels (à droite). Cette méthode permet notamment de

distinguer des patrons ayant la même diversité c'est-à-dire les mêmes fréquences de N éléments mais des distributions différentes dans l'espace (Andrienko, Brilliantov and Kurths, 2000). Les assemblages spatiaux complexes (valeurs intermédiaires de MIG) sont ainsi distingués des assemblages réguliers (valeur faibles) et des assemblages aléatoires (valeurs élevées). Les patrons spatiaux complexes sont définis par cette méthode comme des patrons à la frontière de l'ordre et du désordre (voir les exemples de patrons et la courbe de MIG en fonction de la complexité dans la Figure 0.5 ci-dessous).

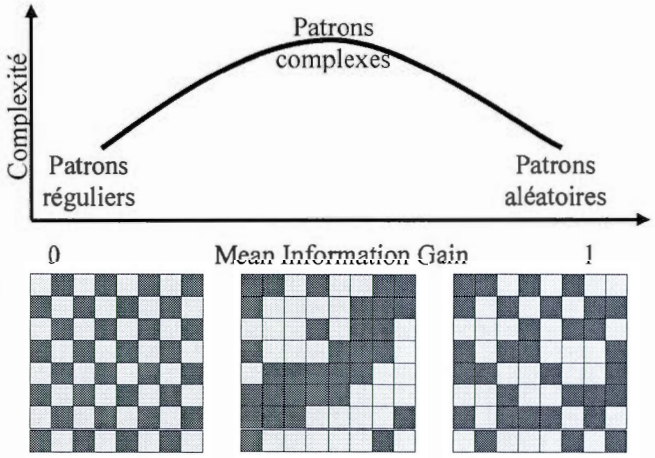

Figure 0.5 Relation entre la complexité des patrons spatiaux et le Mean Information Gain.

Le MIG est en fait un indice de mesure de l'information contenue dans le patron spatial. La valeur finale de l'indice représente la longueur de la description des motifs. Ainsi, un patron régulier qui peut être résumé par la fréquence de la combinaison entre ses espèces aura une description courte : dans notre exemple en damier dans la Figure 0.5 :« 32 x blanc/noir ». Au contraire, dans le cas d'un patron aléatoire, toutes les cases du damier doivent être décrites pour atteindre le même niveau de précision de la description.

Si on admet que les patrons réguliers sont crées par des processus similaires répétés dans l'espace et les patrons aléatoires par des processus aléatoires ou par une superposition anarchique de processus, on peut envisager que les patrons complexes tels que décrits par le MIG sont issus de processus déterministes incluant du bruit ou d'une superposition de processus répondant à une organisation plus lisible. Si ces hypothèses sont admises, on peut également admettre que la mesure de l'hétérogénéité spatiale et fonctionnelle des peuplements forestiers, permet d'évaluer le niveau de complexité globale de ces systèmes (Franklin *et al.*, 2002 ; Habeeb *et al.*, 2005 ; McElhinny *et al.*, 2005 ; Parrott, 2005).

Le choix d'utiliser le MIG dans le contexte de la quantification de l'impact de l'aménagement sur les forêts peut aussi être motivé par son potentiel à être normalisé (grâce à l'utilisation des photographies numériques) et utilisé à grande échelle non seulement dans l'espace mais aussi de façon répétée dans le temps. Le MIG pourrait de surcroît être utilisé à différentes échelles par exemple sur les photos aériennes des peuplements ou sur les distributions de populations microbiennes dans le sol. Cette applicabilité à différentes échelles pourrait faire du MIG un outil permettant de définir les échelles auxquelles les patrons sont les plus déterministes et donc les plus aptes à être modélisés. De plus, son application sur des photographies numérique permet de le confronter directement aux études sociologiques d'acceptabilité dans un contexte d'aménagement écosystémique. Cependant avant d'envisager de tels développements, une première validation du MIG comme indicateur de la complexité des patrons à l'échelle des communautés est nécessaire.

0.4 Les réseaux pour représenter les systèmes écologiques complexes

Au travers de la recherche bibliographique résumée dans les précédents paragraphes, il apparaît que l'introduction de la complexité pour le suivi de l'aménagement forestier implique d'intégrer un certain nombre de dimensions

permettant de replacer les systèmes dans leurs contextes écologiques, temporels et d'échelles.

Cependant, au cours de ce travail, l'utilisation de patrons formés par les objets en fonction non seulement de leurs dimensions individuelles mais aussi de leur voisinage (comme dans le cas de la construction des reliefs de canopée pour le calcul du SCI (Zenner and Hibbs, 2000)) nous a ouvert des perspectives prometteuses en terme de mise en contexte de la description des systèmes. Différents travaux sur les interactions biotiques tendent naturellement à intégrer le voisinages des arbres dans les déterminants de l'identité des individus (telle que définie par l'espèce et les dimensions de chaque individu) (Boivin *et al.*, 2010 ; Ruprecht *et al.*, 2010). De plus, l'idée de représenter les systèmes forestiers au travers de patrons schématiques basés sur les processus et faisant en partie l'abstraction de leurs réelles caractéristiques spatiales nous a orienté sur la piste de la théorie des graphes et donc des réseaux. Les réseaux permettent une représentation simplifiée des systèmes complexes mettant l'emphase sur les liens fonctionnels entre objets (interactions, usage commun des ressources, migrations, déplacements, liens trophiques...). Ces représentations permettent d'associer à un même niveau hiérarchique des objets issus de différentes échelles ou représentant des groupes d'effectifs différents mais partageant la même importance pour le système (en reliant par exemple dans un même réseau un groupe représentant tous les sapin de moins de 20cm de DHP à un unique pin dominant la canopée). Différents travaux sur les réseaux ont notamment démontré que l'étude de la structure émergeante des réseaux (le patron de distribution des connections entre objets) permet de cibler les fragilités du système et donc de mieux préparer les opérations de gestion (Solé and Montoya, 2001 ; James *et al.*, 2005). Cette approche de la représentation de la complexité nous a paru assez intéressante, eu égard à son potentiel de représentation des systèmes forestiers et à son applicabilité aux problématiques de gestion impliquant différentes échelles, pour motiver l'écriture d'un article de revue sur le sujet (Chapitre 1). Cette revue a pour objectif d'introduire

les réseaux en écologie forestière en présentant les principes de base de leur fonctionnement, ainsi qu'un ensemble de méthodes permettant de déduire leur structure à partir des patrons spatiaux.

0.5 Objectifs de la thèse

(1) Développer le point de vue de la complexité en écologie forestière.

En écologie et particulièrement en écologie forestière, la complexité est le plus souvent assimilée à la difficulté de représenter toutes les dimensions du système. Ainsi, l'image du système complexité est utilisée pour appuyer le fait que le système peut se montrer imprévisible et que les signaux mesurés sont inexacts ou imprécis. Cependant, la littérature issue de l'étude des systèmes complexes et des systèmes complexes adaptatifs montre que les propriétés de ces systèmes peuvent être comprises et utilisées pour leur modélisation, et donc par la suite, pour leur gestion.

Le premier objectif de cette thèse sera donc de mettre en évidence l'applicabilité de certains outils et théories des systèmes complexes pour l'écologie forestière. De cette manière, nous espérons encourager les chercheurs en écologie forestière à utiliser les méthodes issues de la complexité.

(2) Proposer une approche originale pour intégrer la compréhension des systèmes écologiques complexes en écologie forestière.

La représentation des systèmes en écologie forestière est depuis longtemps basée sur un emboîtement de sous-systèmes à différentes échelles. Les résultats moyennés des processus agissant à petite échelle sont ainsi injectés dans les modèles à plus grande échelle, les processus agissant à différentes échelles sont ainsi souvent omis, ou intégrés à l'erreur globale du modèle. Une approche différente des relations entre les différents objets processus et les échelles d'étude peut être envisagée.

(3) Améliorer la compréhension des liens entre complexité et hétérogénéité des structures.

Dans la littérature, la complexité est régulièrement associée à la diversité spécifique et à la diversité des structures dans les systèmes. Cependant la connexion entre l'hétérogénéité des structures et la complexité des patrons spatiaux n'est jamais réellement mesurée en forêt. La vérification de cette relation permettrait de mieux comprendre les déterminants de la complexité et peut être aussi de développer une méthode d'échantillonnage commune basée sur les meilleurs indicateurs de la complexité des systèmes.

(4) Développer une méthode pour mesurer la complexité des systèmes forestiers complexes.

L'introduction d'objectifs de conservation de la complexité des communautés forestière en aménagement implique qu'une méthode de suivi opérationnelle soit disponible pour contrôler les résultats. Les méthodes de mesure de la complexité qui existent à ce jour requièrent en général un grand nombre de données et des échantillonnages à plusieurs échelles. Ces méthodes sont par ailleurs basées plutôt sur des séries temporelles sur les résultats de processus écologiques (croissance, fréquence des feux...) ou sur les patrons à grande échelle (paysage). Une méthode utilisable à l'échelle des opérations forestières et qui permettrait de suivre le rétablissement des communautés après les coupes est donc nécessaire. En nous basant sur les liens existants dans la littérature entre complexité et hétérogénéité structurelle (qui caractérise l'ensemble des indicateurs représentant la diversité des structures dans les peuplements forestiers) et sur l'hypothèse selon laquelle la complexité des processus engage un certain niveau de complexité des patrons spatiaux, nous avons décidé de tester différents indices d'hétérogénéité des structures et de les comparer aux résultats du MIG mesuré sur des photographies numériques (Proulx and Parrott,

2008). L'objectif étant de définir quels indices permettent de décrire le plus efficacement la complexité du système.

(5) Evaluer les effets des coupe écosystémiques sur la complexité des forêts mixtes.

Les méthodes d'aménagement écosystémiques incluent le plus souvent des coupes partielles pour mimer les effets des perturbations naturelles et ainsi favoriser les processus naturels de restauration et de maintient de la résilience. Les effets de ces coupes sur l'hétérogénéité des structures et la diversité commencent à être connus mais leurs effets plus globaux sur les patrons spatiaux et la complexité des systèmes sont encore peu étudiés. Un test des impacts des coupes partielles en conditions réelles d'exploitation forestière permettrait d'éclaircir cette question et d'améliorer encore l'impact des coupes sur les systèmes forestiers.

CHAPITRE I

INCORPORATING COMPLEX NETWORK THEORY INTO FOREST MANAGEMENT: A MINI-REVIEW

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1.1 Abstract

As forest managers are now required to incorporate an increasing number of constraints and objectives at different spatial and temporal scales into management plans, they require new approaches and tools to achieve these new demands. One such approach that has been gaining momentum in ecology is complex network theory. The intention of this paper is to review the concepts and theory behind the use of complex networks as recently developed in ecology and to evaluate how they can be applied to forest management.

Networks are defined as simplified systems that are based on the interactions and connections (links) between various elements (nodes). Functionally important nodes are called hubs and bottlenecks and they play a disproportionate role in maintaining or reducing resistance and resilience following catastrophic disturbances of complex systems such as forests. By identifying these functionally important nodes and links and by making sure that they are maintained or replaced over time and space through efficient management interventions, forest managers are more likely to achieve their pluralistic objectives.

The study of fragmentation in forested landscapes is an example where a complex network approach could be used in forestry. The structure of networks in forest systems is often related to the spatial distribution of objects (forest fragments, trees, individual plants...) where the interactions represented as links are limited to relatively small distances. The description of the spatial interconnectedness between forest objects can thus be used to infer forest networks.

The flexibility of such an approach based on a functional representation warrants further investigation. Notably, the definition of a methodology to allow identifying nodes in forest systems needs to be further developed.

Keywords: Forest ecology, Network theory, Complex system study, Community ecology, Forest management, Resilience, Keystone structures, Hubs, Fragility.

1.2 Introduction

Forest management in Canada has long focussed on a few well defined objectives concerned mainly with timber and game production. Forests managers are now diversifying their objectives and are faced with an ever increasing number of socio-ecological objectives that encompass different spatial and temporal scales (Messier and Kneeshaw, 1999 ; Puettmann, Coates and Messier, 2009 ; Heinimann, 2010). Furthermore, growing uncertainties caused by climate change, pollution, loss of habitat and invasive species are relatively recent concerns that must be considered (Vitousek *et al.*, 1997 ; Sala *et al.*, 2000). Clearly, managing forest landscapes has become increasingly complex and requires the development of new approaches able to integrate the numerous interactions and interconnectedness of the parts and processes found in forest ecosystems (Baskent and Keles, 2005 ; Hein and Ierland, 2006 ; Lindenmayer, Franklin and Fischer, 2006 ; Schulte *et al.*, 2006 ; Puettmann, Coates and Messier, 2009). As a consequence, a number of researchers have begun advocating the need for a new approach to managing the forest landscape based on the conservation of the complexity of forests (Puettmann, Coates and Messier, 2009 ; Messier and Puettmann, 2011). Such complexity-based management should allow for the conservation and enhancement of the adaptability of forest systems and hence should be itself adaptable. Complex management should also allow for the integration of multiple scales of organisation and acknowledge the fact that forests are open systems connected to non-forest systems (climate, social systems, hydrological systems...).

Although many efforts are made in research to integrate forest units (trees, communities, plots, landscape...) across scales (Muzy *et al.*, 2005 ; James *et al.*, 2007), the management of the forest system is still planned according to pre-established spatial scales (individual tree, plot, management unit or landscape) with very little consideration for the functional importance of each of these elements in the

whole system. For each of these scale subdivisions, individual elements are normally defined according to their size and not to their functional importance in the system (single trees at the individual scale, management units at the scale of the landscape). These scales of management are also embedded into one another resulting in a "Russian doll" type structure which limits the extrapolation of management from one scale to another as the management units are of different nature at each scale (individual trees, plots, land use units, catchment areas...). The adaptability of rules and policies to small-scale systems is therefore limited as they cannot be propagated to larger areas and are technically difficult to apply locally.

Moreover, with such strictly nested structures, the understanding of processes that act through scales is arduous. For example, typically, biotic interactions are studied at the scale of individuals, considering the effects of competitor plants on their immediate neighbours. On the other hand, larger patterns such as the distribution of species diversity are mainly linked to large scale processes or environmental patterns (dispersal, climate, topology...). These two aspects of ecology (small scale propagating processes and large scale patterns) are thus usually separated by the scales of their study and are therefore often difficult to reconcile. However, different research showed that a part of the variation of large scale patterns could be explained by small scale processes. For example, Wiegand *et al.* (2007) found evidences of community scale effects of plant-plant biotic interactions on tree biodiversity in tropical forests. Some competitive species were thus shown to have a negative effect on biodiversity at large distances (up to 15 metres). Similarly, the propagation of gaps at the scale of forest stands (Vepakomma, Kneeshaw and St-Onge, 2010) was shown to be influenced largely by small variations at the scale of individual trees that have effects at the larger scales (community or forest stand). Evidently such cross-scale effects could interact with management operations and cause unexpected consequences. Nevertheless, these dynamics can hardly be integrated to the current framework of forest management as the causes (interactions between trees and the

distribution of gaps) and effects (variations in diversity, loss of biomass) of these mechanisms are not located at the same scales of management.

Managing for complexity emphasizes the need for new tools that can accommodate a holistic representation of the forest and integrate many hierarchical levels, large number of individuals interacting over different spatial and temporal scales and non-linear dynamics (Messier and Puettmann, 2011). Complex system study offers such a unique framework. This multidisciplinary research field (e.g. physics (Goldenfeld and Kadanoff, 1999), ecology (Levin, 1998), linguistics (Chomsky, 1957), and economics (Mandelbroot, 1973)) aims at the understanding of the processes underlying the self-organisation of systems whose dynamics cannot be derived by superposing the individual dynamics of their components (Parrott, 2002). These systems often show seemingly organised although highly variable patterns in space and time (Levin, 2005 ; Heinimann, 2010). Complex systems are primarily characterised by their seemingly unpredictable behaviours. A field of the study of complex systems thus focused on the development of tools and methods able to properly describe these dynamics and the patterns they create in space and time.

Among the methods put forward by complexity theory, network analysis has been shown to be a useful approach to study the structure formed by the interconnections between individual objects. From neural to social networks, the internet to trophic webs, real-world networks are not randomly wired and share common architectural principles regardless of their size, scale, age or function (Strogatz, 2001 ; Newman, 2003 ; Barabási, 2009). Network analysis provides instructive information that cannot be inferred by investigations at the scale of individual objects (Proulx, Promislow and Phillips, 2005) such as the relative importance of specific objects to network functioning, or the network effectiveness in connecting two separated objects. Network theory therefore offers a beneficial framework to examine the relationships between the structure of a system and its

resilience and resistance to perturbations (e.g. loss of objects or loss of the connections between objects).

In ecology, interest in networks has mainly focused on food-webs (Montoya, Pimm and Solé, 2006 ; Anand *et al.*, 2010). Applications are now beginning to spread beyond who-eats-who connections by integrating non-trophic interactions such as host-parasitoid (Lafferty, Dobson and Kuris, 2006 ; Ings *et al.*, 2009), facilitation, competition and mutualism (Goudard and Loreau, 2008 ; Bastolla *et al.*, 2009 ; Olff *et al.*, 2009). Moreover, network studies combining spatial interactions (Bastolla *et al.*, 2009 ; Olff *et al.*, 2009) and environmental and temporal variations (Raymond and Hosie, 2009 ; Blüthgen, 2010) are also developing. Network theory has also been applied in landscape ecology and conservation biology. In this context, networks represent habitats linked by species dispersal and constitute an effective and flexible tool for investigating habitat connectivity (Urban and Keitt, 2001 ; James *et al.*, 2005 ; Cumming *et al.*, 2010 ; Rayfield, Fortin and Fall, 2011).

Considering the developments of network analysis in ecology we intend to highlight the potential of network thinking for forest ecology and management: First, networks are integrative frameworks that could permit a multi-scale representation of the forest by underlying its various components (plants, animals, forest patches, corridors, isolated trees...) and their interconnections (predation, competition, dispersal ...). This approach could therefore improve our understanding of the relationships between the processes occurring at the local scale (e.g. plant-plant interactions, gap propagation, mycorrhizal exchanges, seed survival...) and the spatiotemporal dynamics emerging at the forest scale (species shifts, evolution, stability, pseudo-cyclic dynamics of disturbances...) (Heylighen, 1996 ; Levin, 2005 ; Proulx, 2006). Second, network analysis could help identifying the components, connections and structural properties most functionally important to forest systems. This could allow for the development of more effective landscape configurations and restoration programs (James *et al.*, 2005). Third, network models could allow for the

development and testing of diverse hypotheses regarding the effects of different harvest operations and natural disturbances on the structure and function of forest. Finally, the structure of networks allows integrating various elements of ecological, economic and social interactions at the same hierarchical level within the same representation. This property could notably aid ecosystem management by integrating the interactions between these three categories of objectives in forest management.

The intention of this paper is to review the concepts and theory behind the use of complex networks as recently developed in ecology and to see how they can be applied to forest management. To do so, we first describe what a network is and how it can be used to represent complex forest systems. In doing so, we will also review some of the key elements and properties of the analysis of networks. We then provide an example of how network theory can be applied to forests using the landscape concept of fragmented forests. Finally, we explore some challenges for an effective integration of network analysis in forest management.

1.3 The notion of "networks" in ecology

> *"What we observe is not nature itself but nature exposed to our method of questioning." (Heisenberg 1958).*

1.3.1 Networks: a representation of complex systems

Networks are simplified systems based on the interactions and connections between various elements. Network models of ecological systems may be extremely sophisticated but are all constructed from the same basic ingredients (for an excellent introduction to network theory in ecology, see Proulx, Promislow and Phillips, 2005). Each element in a network is represented by a node which may be connected to other nodes by links (also known as edges). The nodes are defined by their identity and their connections to other nodes. The nature of the nodes varies according to the research interest and the system under study. In forest communities, nodes can be defined as any individual (tree, understorey plant, animal, fungus...) and the links

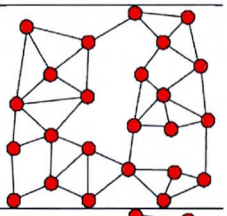
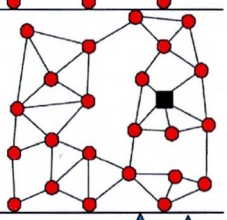
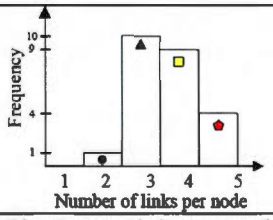
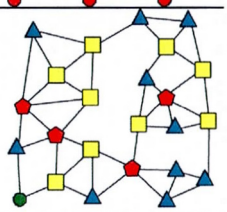
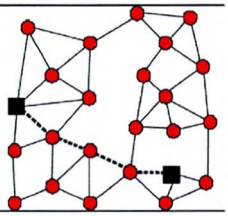
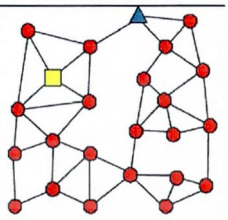
represent the interactions between each individual (predation, competition for light, pollination, animal migration ...). In a landscape, nodes can represent forest sub-systems (i.e. patches) of different compositions or age (pine monocultures scattered with mixed-wood forests and open area) and be connected by animals travelling through corridors of vegetation (James *et al.*, 2005). The links between scattered forest plots may even represent a predetermined maximal distance between similar patches, e.g. two pine monocultures are linked in the network if the distance between them is inferior to a specific desirable range. The distance of reference may even vary depending on the composition of the surrounding community for example, if the density of pines mixed within that community is superior to half of the total tree density, the maximum distance allowing a link to exist between two pine monocultures can be increased proportionally. The links between nodes may be unidirectional (e.g. predation links in a food web) or bidirectional (e.g. birds travelling back and forth between two forest habitats or fungus propagation between different slash piles). Links can also be weighted to express the strength of an interaction (e.g. a predator's relative preference for a given abundant prey) (Proulx, Promislow and Phillips, 2005).

Multiple statistical measures can be extracted from networks and be used as indicators of the systems structure and function. We list here a few fundamental measures (summarized in Table 1.1) – a more in-depth discussion can be found in Newman (2003), Rayfield, Fortin and Fall (2011) and Strogatz (2001). The total number of nodes (N) and the total number of links (L) composing a network can be used to calculate the average number of links per node (L/N) and the network connectivity (L/N^2). The number of links for a given node constitutes its degree. The degree distribution of a network is commonly employed to characterize its topology. The sum of all consecutive links joining two nodes is called a path. The path represents the number of indirect interactions necessary for one node to influence the other. The degree separation measures the average path length between two nodes,

while the diameter of a network is the average shortest path between all pairs of nodes. Finally the clustering coefficient measures the tendency of local nodes to gather together and is calculated by the proportion of interconnectedness among neighbouring nodes (see Table 1.1). These indices allow the evaluation of the diversity of the forest elements that interact in the system (N and L) and the capacity of individual forest elements (individual trees or forest patches) to influence the network at large scales (path, average path length and diameter). Important nodes and structures can also emerge through the analysis of these indices (e.g. clusters may be identified using the clustering coefficient). More generally these indices help reveal the structure of organisation of the network which in turn contains information regarding its robustness and the importance of specific forest elements.

Using a simplified typology, the structure of a network can be classified along a randomness gradient from totally regular (Figure 1.1.a) to totally random (Figure 1.1.c). Complex networks are found at an intermediate level between these two extremes (Figure 1.1.b). Regular networks are highly ordered with all nodes having the same degree (number of links), whereas random networks follow a Poisson degree distribution. Complex networks have an uneven degree distribution characterized by a long tail: a majority of nodes being poorly connected and a small number of nodes being highly connected (Figure 1.1.b bottom graph) (Jordán and Scheuring, 2004 ; Proulx, Promislow and Phillips, 2005).

Table 1.1 Summary of basic measures for the analysis of the structure of network systems. Red circles and other shapes represent the nodes, and the lines represent the links.

Index		Example network
N: Total number of nodes	N = 24	
L: Total number of links	L = 44	
L/N: Average number of links per node	L/N = 1.83	
L/N^2: Network connectivity	$L/N^2 = 0.08$	
D: Degree: the number of links for a specific node	Degree for the black square: D = 5	
Degree distribution: The representation of the frequency of degrees in the network		
Path: The number of consecutive links necessary to join two nodes	Shortest path between the two black square nodes (dashed line): 4 links	
Degree separation	Average path length between two nodes, considering all possible paths between them.	
Diameter	Average shortest path length for all pairs of nodes in the network.	
Clustering coefficient: Proportion of realized links Li over all possible links among the N_i neighbours of a given node i $Ci = \frac{L_i}{N_i (N_i - 1) / 2}$	For the yellow square: $Cs = \frac{4}{4 (4 - 1) / 2} = 0.67$ For the blue triangle: $Ct = \frac{1}{3 (3 - 1) / 2} = 0.33$	

The degree distribution of complex networks may be exponential or follow a power-law. Numerous real-world networks (world-wide web, social interaction networks...) exhibit such a complex structure and this discovery has generated much interest in network theory over past decades (Barabási, 2009). The emergence of a random structure in a forest network more likely results from the absence of regulation processes (feedback loops, criticality thresholds, large scale disturbances, stresses causing reduced fitness or mortality...). Regular networks rather reveal the effects of strong regulation processes or anthropogenic organisation. Complex networks combine strong organisation processes – that can create redundancies of paths and intermediate levels of organisation in clusters (for example in forest sub-systems or microhabitats) – and some unpredictable processes that bring variability to the connections between nodes therefore preventing reliable predictions of the systems dynamics (Hutchinson, 1953).

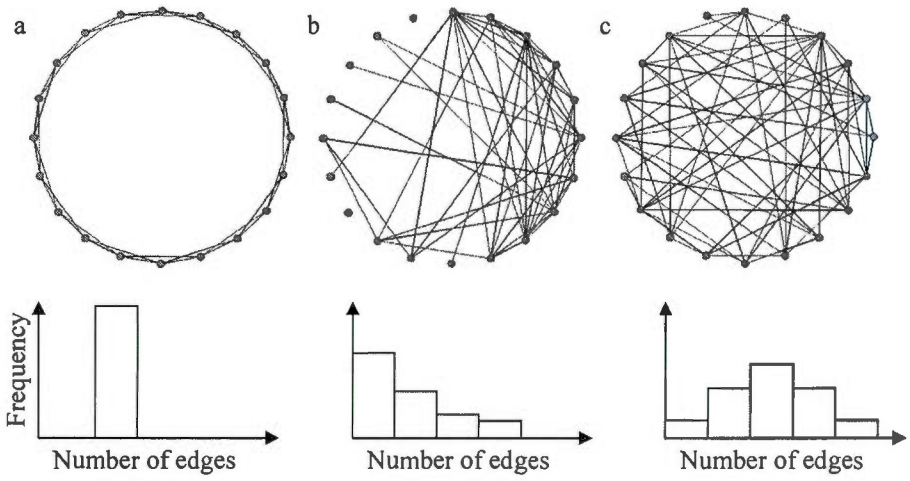


Figure 1.1 Examples of three networks varying from totally regular to totally random. The overall structure of the network (top figures) is captured by its degree distribution (bottom figures): a) Regular (all nodes bear the same number of links), b) Complex (the degree distribution has a fat-tail which may fit a power law or an exponential distribution) and c) Random (the degree distribution follows a Poisson distribution) networks.

Networks may also serve as a strong visualisation tool. Different representation schemes exist. The position of nodes in a landscape network can be defined by the spatial position of the elements in the forest. Node coordinates can also be computed in order to represent a specific feature of the network structure. Networks can thus be represented with their nodes projected along a circle to better visualise the distribution of links and the structure of the network (Figure 1.2.a). The projection can also be designed to reduce the average length of links (Figure 1.2.b) which will emphasize the functional proximity of different nodes. Otherwise, the projection can be organised according to the identity of nodes (e.g. by species, size, age or functional traits) or to the spatial distribution of the forest objects represented by the nodes. Network projection integrates the complexity of the interconnections between the various system elements. The overall structure or patterns emerging from a projection can reveal insightful information about the global functioning and resilience of the system. For example, specific arrangements of nodes in a projection minimizing the length of links (like in Figure 1.2.b) can reveal the existence of a cluster of objects that interact closely together, whether because they all share functional characteristics (e.g. all xylophage insects related to a node representing dead wood) or because they are spatially related (e.g. an assemblage of individuals grouped within a gap).

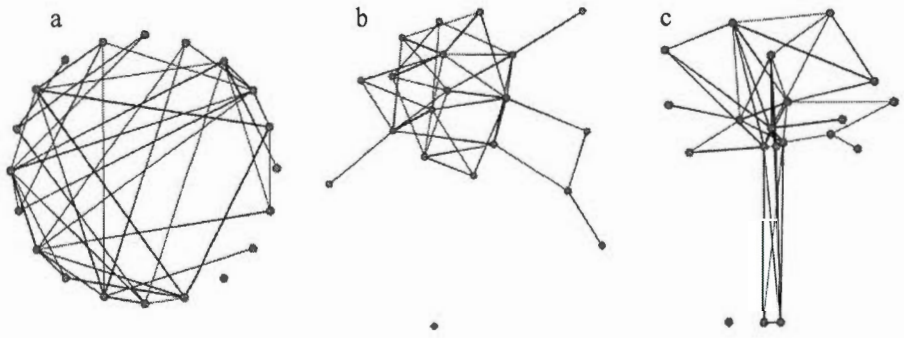


Figure 1.2 Examples of network projections: a, b and c are three representations of the same random network of 20 nodes (dots) having an average of 4 links for each node. a) a circular representation with nodes randomly distributed along a circle, b) a Fruchterman-Reingold projection which forces the distribution of nodes to minimize link crossings (black line linking two nodes) and to equalize the lengths of links; c) a distribution of nodes according to preset coordinates. These coordinates may correspond to the actual position of nodes in space.

1.3.2 Not all nodes are equal

In networks, not all nodes are equal. Some nodes or arrangement of nodes are more significant to the system's function than others. The least connected nodes are dead ends (triangles in Figure 1.3). They have low degree and are therefore at high risk of being isolated or going extinct. These nodes are rare in regular or random networks, but constitute the majority of the complex systems nodes. Dead end nodes have low importance for the overall structure and functioning of the network and may act as 'fuses' to protect the core of the organisation in case of disturbances. In food-webs, dead-ends may be species unpalatable or too small for consumption. In forest landscapes, they may be patches linked by a single corridor to other forest components or a rare species that has very little influence over the rest of the community.

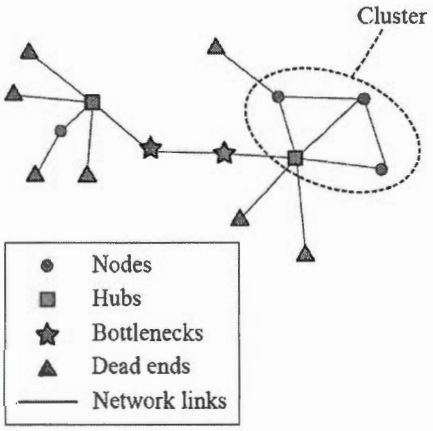


Figure 1.3 Remarkable nodes: Different characteristic nodes may emerge depending on the overall structure of the network. The most connected nodes are called 'hubs' (squares in the figure) whereas the least connected nodes ending paths are 'dead ends' (triangles). Bottleneck nodes (stars) are also poorly connected but are functionally important as they guarantee the cohesion of large parts of the network. Clusters are structures that emerge from the interconnections within a group of nodes (within the dashed ellipse). They can reveal sub-systems with a specific organisation.

At the other extreme, the most connected nodes are called 'hubs' (see square nodes in Figure 1.3). In random networks, where most nodes are connected by a close-to-average number of links, hubs are rare and have a minor influence on the network functioning (Figure 1.1.c). In complex networks however, while hubs are also rare, they play an important structuring role, as they centralize most of the system's paths (other nodes being poorly connected) Figure 1.1.b). Moreover, these complex network hubs, allow short paths to form across the system, linking distant nodes with a smaller number of connections than in a regular network. In forest systems, some species of generalist pollinator that propagate over large distances may act as hubs as they allow the maintenance of several species and are therefore connected to multiple other nodes. Hubs are often related to some key species that play a pivotal role in the functioning of the system. For example, 'keystone species' have such a strong influence relative to their abundance (either as key predators,

preys or mutualist species) that their disappearance would cause a shift in the dynamics of the community or ecosystem resulting in variatons in their composition (Paine, 1969 ; Mills, Soulé and Doak, 1993). 'Keystone species' are often generalist predators (e.g. sea otters) that tend to control the populations of a large number of prey species and thus indirectly regulate the population of other predators. These species are connected to a large number of other species through different trophic interactions and could be compared to highly linked hubs. Similarly, 'ecosystem engineers' (Jones, Lawton and Shachak, 1994 ; Hastings *et al.*, 2007) through their ability to transform the local conditions have a determinant impact on their community. Engineer species like trees, beavers or corals, facilitate the establishment and survival of many other species, and could also be represented as hubs as they are connected to most of the new members of the community.

Clusters are specific arrangements of nodes found in complex networks. A cluster is a group of highly interconnected nodes only connected with the rest of the network by a small number of links (Figure 1.3). Clusters can remain unnoticed unless the structure of the network is studied as a whole. A high clustering coefficient and a short network diameter (Table 1.1) are good indicators of their presence. For example, sub-communities related to micro-habitats like wetlands or the assemblies of ruderal species found under forest gaps can be examples of clusters as the nodes representing each species will be more connected to nodes with similar ecological requirements than to the rest of the forest community. The existence of clusters and hubs generally indicates the presence of special nodes, called bottlenecks (stars in Figure 1.3), that connect (or separate) these groups of nodes from the rest of the network. Again, bottlenecks cannot be identified from the degree distribution alone, and require an observation of the entire network. In forest networks, bottleneck can take of different forms. A hedgerow allowing the connection between two forest patches can be a bottleneck if it constitutes the only passage for the fauna. Also a bird species with a long range of movement can be represented as a rare communication between two

communities. Some engineer species (Jones, Lawton and Shachak, 1994 ; Hastings *et al.*, 2007) may also be considered as bottleneck nodes as they connect sub-systems or clusters to the main network. For example, brown bears allow a connection between aquatic and terrestrial compartments of forests through their consumption of salmons and the discarding of their carcasses which fertilises riparian bands (Hilderbrand *et al.*, 1999). Like dead ends, bottlenecks have a low degree. However, they have a greater impact on the structure and function of the network as they are the key pathways linking the fundamental network components. Because of this property, a bottleneck can also be a particularly vulnerable element of a network.

The same forest element may be viewed as a hub, a cluster or a bottleneck node depending on the research question and the scale of the study. For example, residual clumps of trees in a recent clear-cut (following variable retention harvesting) could be considered to be hubs because they will attract several other organisms that require covered environments. Forest clumps can also be considered to be cluster since they constitute a seemingly independent group of interconnected trees in an otherwise herbaceous dominated community networks. Finally, they can form a bottleneck node that connects other clumps of trees in the clear-cut. In this example, each clump of trees can actually be considered to be an assembly of individuals or a single structure, depending on the level of details one wants to represent. As a consequence, it is important to clearly define what a node represents in forest networks as this will affect the distribution of links and thus the role of each node in the system.

1.3.3 Fragility of networks

The overall structure of networks (see Figure 1.1) and the distribution of hubs, bottlenecks and clusters Figure 1.3) are particularly important for the dynamics of networks as they influence the fragility of the whole system. Research on networks (from the internet to lake food-webs) has demonstrated that the random removal of nodes has different effects depending on the structure of networks (Albert, Jeong and Barabasi, 2000 ; Solé and Montoya, 2001 ; Montoya, Pimm and Solé, 2006).

In regular or random networks, the impact of random node removal is proportional to the number of removed nodes, whereas in a complex network it is dependent on the probability of the removal of hubs. As a consequence, the total size of the network tends to decrease more steeply in regular or random networks (indicating fragmentation) Figure 1.4.2b) than in complex network (Figure 1.4.1b). In complex networks as only a relatively small proportion of nodes (the hubs) are essential to the conservation of the structure of the whole network, the majority of nodes may be considered as a mechanical protection against the random removal of hubs. As hubs are rare by definition, they are less likely to be randomly removed and the structure is therefore more robust.

Evidently, if the deletion of nodes is selective and targets the most connected nodes, the consequences in complex networks are dramatic, causing a rapid fragmentation of the system and the extinction or threat of extinction of isolated elements (Solé and Montoya, 2001) Figure 1.4.1a). This effect of fragmentation actually occurs at a quicker rate in complex network than in random systems where the structure consists of nodes with an average number of connections Figure 1.4.2a) (Albert, Jeong and Barabasi, 2000). Hence, when managing a forest system organised according to a complex network, hubs as well as bottlenecks should be carefully identified and managed to conserve the structure of the network. Specifically, for those unique nodes to continue achieving their significant functional roles, as many links as possible must be preserved between them and the rest of the system. In other words, complex forest management should be based on the identification of important elements (nodes, hubs, bottleneck...) and of their context in the network and focus their entire management around those elements.

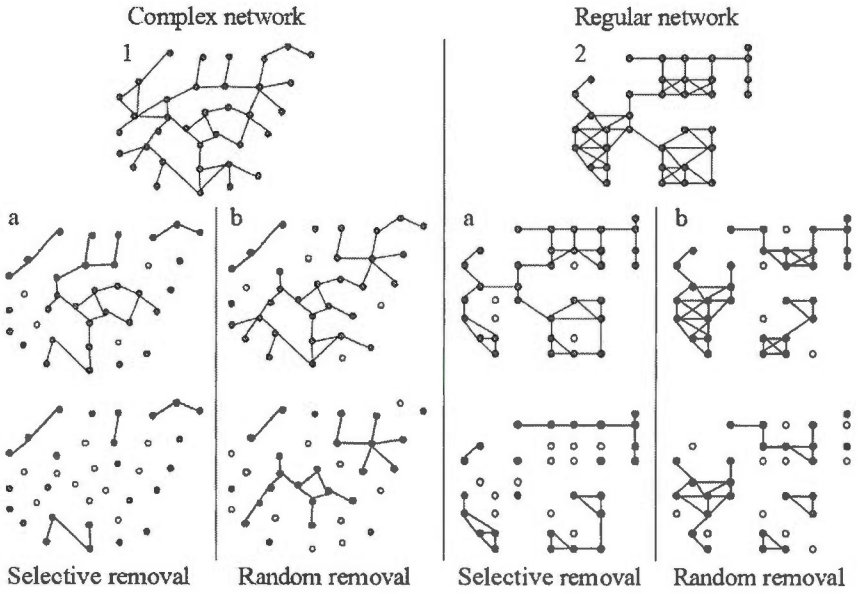


Figure 1.4 Illustration of fragmentation mechanisms in complex (1) and regular (2) networks under selective removal of the most connected nodes (a) and random removal (b). Open circles represent the nodes that were removed. Complex networks are sensitive to the removal of the most connected nodes (1a), and the system is quickly reduced to small fragments. In the case of random removal, (1b), larger pieces of the network remain. Regular networks (2), on the other hand, show similar responses to both targeted (2a) and random (2b) removal of nodes as remaining networks are relatively large in both cases.

Disturbances may also induce the emergence of new hubs that replace the hubs that are selectively or randomly removed from complex networks. New hubs may also appear if the configuration of links is modified as a result of changes in the dynamics of the system following the degradation of the system. The identity of these new hubs is obviously dependent on the order in which former nodes are removed from the system. During this mechanism, the complex structure of the network may or may not be conserved and most importantly, the nodes that become new hubs are likely to have a different influence over the system than the former hubs. Hence, the conservation of a hub-based structure in the network is not a guarantee that the

system will conserve the same species composition and functions especially if the initial hierarchy of nodes is not preserved.

These theories derived from the study of the fragility of networks are already applied to food webs to demonstrate the importance of keystone and engineer species and develop adaptive management plans, protection or restoration policies (Paine, 1966 ; Hogsden, Xenopoulos and Rusak, 2009 ; Reiss *et al.*, 2009). Moreover, the development of functional ecology in plant communities also tends to confirm the idea that species bear different weights in the functioning of communities depending on their traits and on the traits that are already present in the assembly of species. Hypotheses about functional redundancy thus suggest that only a fraction of the species present in a community are necessary to maintain overall ecological functions (Lawton, 1994 ; Peterson, Allen and Holling, 1998 ; Allen, Gunderson and Johnson, 2005). Obviously, once a system has been degraded, the species that may further be removed from the system depends on the traits of the species that have already disappeared. If the traits of species and individuals are considered as indicators of the processes through which these individuals interact with their neighbours, the comparison with nodes that have different number and quality of links in a network is straightforward. The disappearance of a species bearing functional traits allowing it to interact with a large number of other individuals should thus cause a large decrease in the functional efficiency of the system and thus a significant loss in its resilience. On the other hand, if all species in the system share similar traits (meaning that every species has an average ascendancy over the other individuals) the disappearance of one species should be less critical as this species is not likely to be a hub.

The understanding of network fragility could ultimately be developed to create measurable indicators of the resilience of ecological systems as defined by the amount of disturbance that would induce a shift in the composition or functions of the system (Holling, 1973 ; Gunderson, 2000). For example, for a given type of disturbance (random removal, targeted removal of hubs or of species…) the number

of nodes that can be removed from the system before its size (network diameter) or structure (connectivity, clustering) is significantly affected (Albert, Jeong and Barabasi, 2000). Variations in the hierarchy of nodes (from most connected hubs to the less connected nodes) could also be used as an indicator of resilience as it will reflect the composition and diversity of species in the network.

An additional dimension of the resilience of networks could also be derived from their capacity of reorganisation after nodes loss. This capacity could for example be quantified as the variation in the shape of the degree distribution (from power law to constant or Poisson distribution) that reflects the overall structure of the system (Albert, Jeong and Barabasi, 2000 ; Solé and Montoya, 2001). Hence, the adaptive capacity of forest systems (Gunderson, 2000) could be evaluated through changes in the structures of the network regardless of its size (e.g. as expressed by its diameter, see Table 1.1).

Using network formalism, various management scenarios (random, targeted, spatially regular or following different patterns from stripes to patches...) could be tested on network models of different structures (random, regular, complex) to evaluate their resilience and adaptive capacity. Testing this approach would probably allow a better understanding of the effects of different management methods on the structure of systems and thus maybe help to anticipate their effects on patterns at larger scales.

1.4 Applying network theory to forest systems

While network theory is a relatively new concept in ecology and conservation ecology, several successful applications can already be found in the literature on landscape management (Cumming *et al.*, 2010 ; Rayfield, Fortin and Fall, 2011) and community ecology (Montoya, Pimm and Solé, 2006 ; Sugihara and Ye, 2009). These ecological studies highlight the potential of network thinking in forest ecology and management.

In a forest management context, network analysis could be used to identify various important nodes (such as hubs and bottlenecks), notable arrangement of nodes (clusters) and the overall structure of the forest network (random, complex or regular). This knowledge would allow for the development of more effective landscape configurations and restoration programs by identifying and then more efficiently managing the most functionally important elements of the system. Moreover, with the understanding of how hubs and bottlenecks can emerge or disappear according to changes in the overall structure and functioning of the network (following a large fire, road construction, the presence of an invasive species or changing climatic conditions), better and more effective interventions can be planned to maintain as much as possible the resilience of the system.

1.4.1 Composite elements as nodes

The construction of a forest network model begins with the identification of nodes. Nodes may be any forest element, and thus represent single individuals or group of individuals (see a list of example in Table 1.2). Considering each individual tree as a node in a forest community, would tend to create a regular network defined by the distances between individuals and their sizes. Nodes might also represent groups of individual trees assembled according to a common influence on the community (similar trophic position in foodwebs for example) (Ings *et al.*, 2009 ; Raymond and Hosie, 2009) or with regards to similar connections to other nodes (thus grouping species that are commonly found as companions). Although species provide a natural unit for grouping entities in ecology, aggregating individuals strictly according to their species is not necessarily relevant in forest network modelling. For example, two large coniferous trees of two different species may have a more similar effect on the system and thus more similar connections to other nodes than an adult tree and a seedling of the same species.

Links in a forest network could be determined both by a node's function in the system and/or by its spatial proximity with other nodes (see Table 1.2). In the later

case, the degree of a node will depend on the spatial distribution of its neighbouring nodes. Defining links by spatial relationships between nodes could also help constructing networks of forest systems for which some functional relationships are unknown. Hence, the links can be preliminary defined by proximity and then refined to progressively integrate the functions and traits of the nodes that explain their interactions. Recent observations of spatial pattern have focused on the distribution of specific structures such as gaps (Lamonaca, Corona and Barbati, 2008 ; Vepakomma, Kneeshaw and St-Onge, 2010), dead wood (Angers *et al.*, 2005 ; Marage and Lemperiere, 2005), forest edges (Watkins *et al.*, 2003 ; Harper *et al.*, 2004) or residual trees (Zenner, 2000). These structures are believed to have a disproportionate influence on the overall functioning of the forest through their effects on other forest organisms (birds, insects) and on different processes (dissemination, seeds installation success...) at the scale of the whole community (Lindenmayer, Margules and Botkin, 2000 ; Marage and Lemperiere, 2005 ; McElhinny *et al.*, 2005). The importance of these structures for the system often appears linked to their functional distance from the surrounding elements. For example, a residual tree is only important for the system as long as its neighbours are significantly smaller or younger and a single large snag loses its importance after disturbance events create large quantities of dead wood.

A similar observation in community ecology also led to the development of the idea of 'keystone structure' (Tews *et al.*, 2004). This concept is an adaptation of both autogenic engineer species (Jones, Lawton and Shachak, 1994) and keystone species (Mills, Soulé and Doak, 1993). The use of keystone structures as elements of biodiversity allows for the accounting of associations of traits borne by different individuals at the same level as species when considering functional diversity. Such keystone structures are defined by their function, but also and more importantly by a significant functional distance from the surrounding system (scattered trees in savannas, dominant trees in even-aged forests, large dead trees in young forest

stands...). They often appear as catalysers of diversity as their function in the community is enhanced by the uniformity of the surrounding community (Tews *et al.*, 2004 ; Manning, Fischer and Lindenmayer, 2006 ; Simila *et al.*, 2006). The spatial distribution of the different structures in the system therefore has an important influence on the definition of keystone structures as they are mainly defined by the composition of their neighbourhood. Recent work even suggests that the information contained in variations in the spatial distribution of elements within a few meters of individuals targeted for conservation could be used to develop adapted management methods as biotic interactions can influence the survival of endangered species (in this example, English yew) more than environmental limitations (Ruprecht *et al.*, 2010). At larger scales, research using LIDAR data in boreal forests to precisely map the canopy also showed the importance of spatial patterns in canopy openings for the creation and propagation of new gaps (Vepakomma, Kneeshaw and St-Onge, 2010 ; Vepakomma, St-Onge and Kneeshaw, 2011). These works and the concept of keystone structure show that the interest for the spatial distribution and the dynamics of forest elements is increasing. Patterns are not only considered as indicators of dynamics but also as determinants of the dynamic of communities and their resilience.

Keystone structures like large dead-trees or dominant trees could be represented as nodes (Table 1.2) in networks and even emerge as hubs as they have an influence over a large number of other individuals (nurse individuals connected to intolerant species, dead-trees connected to many species of insects and fungus...). In addition, if the effects of keystone structures attracts new nodes to the system, their effects as hubs may even increase with time as it is likely that they will be connected to most of the new nodes that join the system (Proulx, Promislow and Phillips, 2005). Moreover, some keystone structures (just like engineer species) could also appear as 'bottleneck nodes' acting as corridors for animals commuting between different communities (notably birds and insects) or for seed propagation in fragmented systems (scattered trees between isolated fragments of forest, woody edges in agricultural landscapes...)

(Collinge, 2000 ; Hunter, 2002 ; Tews *et al.*, 2004 ; Manning, Fischer and Lindenmayer, 2006 ; Levin *et al.*, 2009). Keystone structures are thus important for the functioning of the system and can be hubs not only because their connectivity to other compartments is large, but specifically because they are *more* connected than their neighbouring nodes.

More generally, although the definition of a structure is flexible (as it may vary between systems, spatial scale and research questions) and must be handled carefully, keystone structures allow the consideration of single significant individuals (a dominant tree for example) at the same level as a coherent ensemble of elements (e.g. a group of individuals around a pond, all individuals of a given species or all trees bearing cavities regardless of their species...). In a network, distinct individuals like dominant trees could even be grouped with other individuals from the same clump to represent a single node (likely a hub) in the network. However these same individuals could be represented a second time on their own (in the same network or in a different representation of the network) with the purpose of characterising connections that are independent from the clump structure. Also the same individual is likely to belong to different types of structures depending on the scale at which the system is observed: a single tree could be a structure in itself at a small scale, but become a component of a node including the entire residual forest plot at the scale of the landscape. The role of such structures within an otherwise homogeneous network of interactions can be crucial to the evolution of that system, although their own direct contribution to diversity may be low.

Table 1.2 An example of nodes and corresponding links. These different types of nodes and links could even be combined (e.g. associating a trait similarity and maximum distance to establish a link between two nodes).

Possible nodes	Potential links	Example of links
Species The nodes represent all balsam fir, white spruce or red maple…	Interactions	General relationship between two species: Trophic links, Mutualism, Parasitism…
	Trait similarities	Links can be any common trait or combination of traits between the two species (leaf area index, stem density, dispersal mechanisms…)
Individuals Each individual object is a node: tree, dead tree, understorey plants, fungus…	Proximity	Link depending on the distance between the two individuals
	Interactions	Competition, Facilitation, Interference, Trophic links, Mutualism, Parasitism…
	Trait similarities	The difference between Leaf Area indices between two individuals can determine the strength of the connection
Functional groups Grouping individuals according to functional traits: coniferous, carnivorous, pollinators…	Interactions	General relationship between groups: Trophic links, Mutualism, Parasitism, Interference
	Trait similarities	Connecting functional groups according to their shared traits
Structures Each large dead tree, dominant tree… is represented as an individual node	Interactions	Effects of the structure on other nodes: attraction or repulsion of species, habitat, nutrition
	Proximity	The structures are connected if they are closer than a pre-specified distance
Sub-communities Sub-systems associated with a micro-environment: ponds, wetlands, rocky areas…	Interactions	If some elements in the sub-communities are connected to elements of other surrounding sub-communities
	Animal movements	Depending on the movements of animals between sub-communities
Forest patches In fragmented forest each remnant forest area or clump of trees that originated from the same forest	Proximity	The structures are connected if they are closer than a pre-specified distance
	Animal movements	Depending on the movements of animals between sub-communities

1.4.2 Fragmented forests as an example of network: hubs, bottlenecks and resilience

Although ecological systems can be naturally fragmented (islands, forested savannahs, ponds…), managed forests tend to be even more fragmented as a result of both natural and anthropogenic disturbances and road construction. Different research on forest fragmentation has shown the effect of the shape and area of forest fragments or of the spatial distribution of key elements (roads, openings...) on different forest compartments. Effects of landscape spatial patterns were notably measured on understorey plant species (Honnay, Hermy and Coppin, 1999 ; Watkins *et al.*, 2003), birds (Loehle *et al.*, 2005) and insect populations (Hunter, 2002). The importance of the connections between forest fragments (animals circulation, green corridors) for the maintenance of a functional community led to the emergence of the notion of the metacommunity (Leibold *et al.*, 2004). The development of this concept in turn brought landscape ecologists to the observation of the structure of spatial patterns and to the use of network theory as a means of representing the systems (Bunn, Urban and Keitt, 2000 ; Urban and Keitt, 2001 ; Jordán and Scheuring, 2004 ; James *et al.*, 2005 ; Rayfield, Fortin and Fall, 2011). The study of such networks revealed a strong dependency between the structure of the spatial pattern (the spatial, functional and hierarchical distribution of forest elements), and the robustness and resilience of the network system. The representation of forest systems or landscapes as networks of interacting elements has already allowed the identification of forests fragilities and management hotspots that require special attention (Urban and Keitt, 2001 ; James *et al.*, 2005).

At the landscape scale, fragmented forests are traditionally described according to the size, shape, composition and spatial distribution of the different fragments of closed forests. The identity of the surrounding environment (recent clear-cuts, agriculture, plantations, etc.) in the matrix is also often included in the description of fragmented forests.

When these forest landscapes are considered as meta-communities, an ensemble of processes can also be used to describe the different fragments of a forest with regard to their functional roles in the overall landscape or system (diversity sinks or reservoirs, risk of extinctions or evolution in forest fragments as expressed by their distance from the original population...) (McArthur, 1972 ; Leibold *et al.*, 2004). Most of these processes at the scale of the meta-community actually depend on the spatial distribution of the fragments (nodes) and on the connectivity (i.e. links) between the different fragments. The description of forest fragments can therefore easily be expressed as networks (Proulx, Promislow and Phillips, 2005).

In forest ecology, the definition of the forest objects that are considered as individuals is a subject-oriented decision (Raymond and Hosie, 2009). The identity of these objects that would be represented as nodes is therefore defined at the same time as the questions of research (species of predator or preys, mutualist species, interacting individuals...). The links between these nodes are then defined according to criterion based on previous research or on field investigations (trophic links, mutualist relationship, animal circulation...). In the case of the application of networks to landscape fragmentation or even to plant-plant interactions, the nodes and links can also be deduced from the spatial patterns (Bunn, Urban and Keitt, 2000 ; Urban and Keitt, 2001 ; James *et al.*, 2005). The identification of nodes in fragmented managed forests is facilitated by the existence of discrete structures (forest fragments, scattered trees...) contrasting from the surrounding matrix (younger forest, fields, clear cuts...). This approach to the definition of nodes is original even in the context of network theory as it is not only the structure of the network that emerges from the study of spatial patterns but also the composition of the nodes.

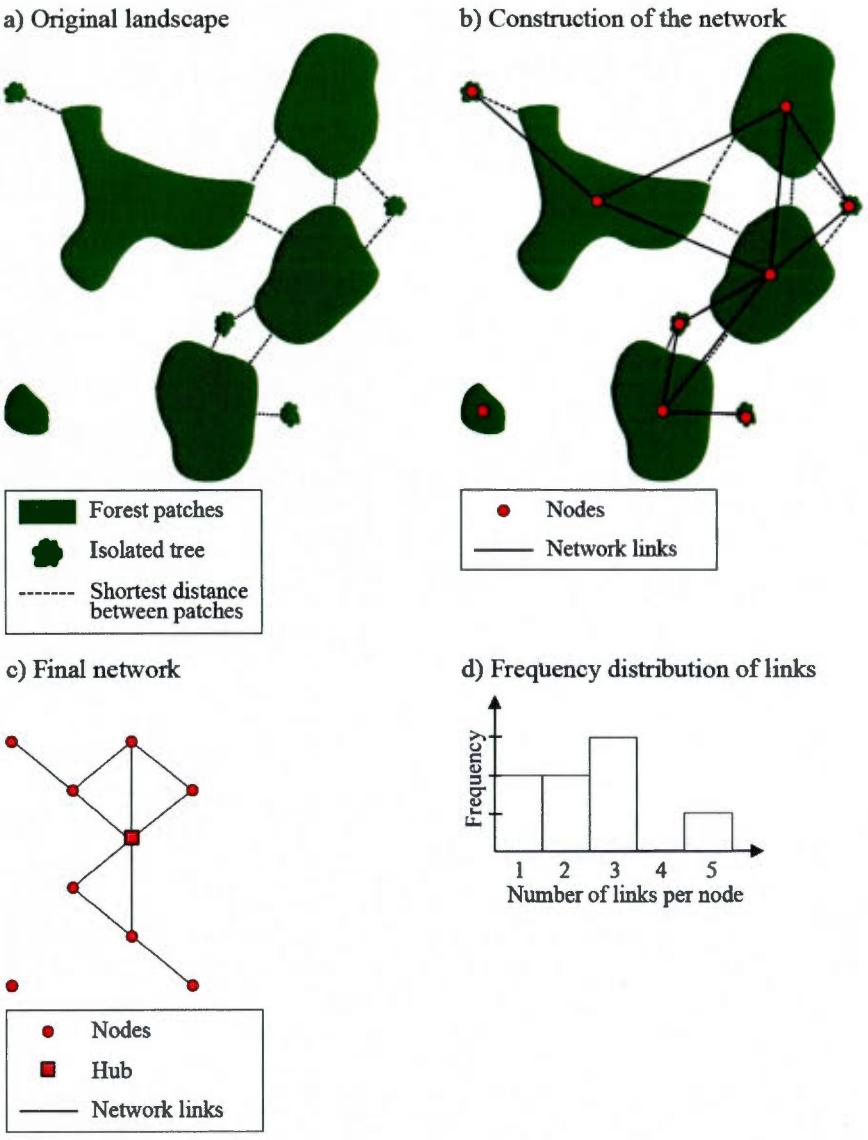


Figure 1.5 An example of the construction of a network from a spatial pattern of fragmented forests. In this example, each fragment of forest is considered as a node. The links exist if the shortest distance between two forest fragments is smaller than a given threshold. The final network presents a hub with degree = 5. Interestingly, that hub does not correspond to the largest fragment, but rather to a smaller more central fragment of forest.

Nodes can therefore be defined by simple criterions regarding the difference between the matrix and nodes (height, number or DBH of trees, species composition, minimum area of the fragment ...). For example, in research based on aerial photographs, each structure with a continuous canopy can be identified as a node (including forest fragments or even individual trees if one can recognise them) (Levin *et al.*, 2009). Hence, in some cases, one single tree may be represented as a node and be hierarchically equivalent to a larger fragment of forest (a large pine, for example) (see Figure 1.5 for an example of the construction of a network from a simple fragmented forest).

Nodes may therefore represent forest fragments of varying sizes and composition in the systems and are only differentiated in the network by their connectivity to the other elements. It is likely that some fragments of forests, notably the largest in surface area, will bear a significantly higher number of links than average. If so, they will emerge as hubs therefore indicating a complex structure in the organisation of the network.

In the characterisation of forest landscapes as networks, it is important to define precisely what function the hubs hold in the network. They are often identified as biodiversity reservoirs, or more largely as providing many key ecosystem services, although the strict definition of reservoirs would require some notion of the size and composition of forest fragments to be confirmed. Hubs can also be rare structures that are necessary as habitat for a large number of other organisms or processes. A large dead tree for example is likely to emerge as a hub as such structure is often rare in the vicinity of managed forests and can be important to several groups of well connected organisms like birds, insects or fungus (McGee, Leopold and Nyland, 1999 ; Greif and Archibold, 2000). Moreover, hubs may also indicate centralised structures such as a network resembling continent-island systems as in biogeography theory (e.g. any large fragment of forest left uncut in a managed landscape and connected to smaller fragments) (McArthur and Wilson, 1967). As hubs are highly connected to the system,

they are also statistically more at risk for pest infestations, diseases, pathogens or fire propagation. More importantly, meta-communities organised around hubs may be at a higher risk for rapid fragmentation should those hubs be eliminated (Solé and Montoya, 2001). Management plans adapted to these structures are therefore crucial for their conservation.

A network based on fragmented forests is also likely to allow the emergence of bottleneck nodes. Although hubs may additionally be bottlenecks, these nodes do not necessarily bear a large number of links, but their position in the structure makes them obligate passages toward distant nodes or sub-systems (James *et al.*, 2005). In fragmented forests, bottlenecks can be green corridors (riparian strips, hedgerows, buffer strips...) between two large fragments of forests (Tewksbury *et al.*, 2002) and thus become obligatory passages for organisms commuting between fragments. The loss of bottleneck nodes might cause a large decrease in the size of the network and ultimately the extinction of disconnected populations (Solé and Montoya, 2001 ; Urban and Keitt, 2001) (Figure 1.3 and Figure 1.4). Much like hubs, bottlenecks can therefore be critical nodes that require some special protection and the need for restoration while managing fragmented forests.

The idea that the importance of each forest fragments is not only dependent on their identity (size, composition, shape...) but also on their position in the network and therefore on their spatial relationship to other fragments is central to most work in landscape ecology. However, even the most integrative management planning for fragmented systems at the scale of the landscape is still often based only on the consideration of the size (minimum viable sizes, percentage of total area under management) and composition (old forests, umbrella species, rare species or specific structures like rivers or ponds...) of forest fragments (Siitonen, Tanskanen and Lehtinen, 2002 ; Côté *et al.*, 2010). The influence of fundamental ecology and its long history of description of patterns to infer processes (evolution, island biogeography (McArthur, 1972), interactions (Tilman, 1982), coexistence (Tilman,

1994 ; Condit *et al.*, 2000 ; Davies, Grenyer and Gittleman, 2005) and functional equivalence (Hubbell, 2006)) could help to rationalise the development of networks based on the study of spatial patterns. The development of an approach of the construction of networks based on spatial patterns could notably help predict the future influence of spatial patterns on the processes mediated through the interactions between nodes (Turner, 1989 ; Kramer-Schadt *et al.*, 2007 ; Fraterrigo, Pearson and Turner, 2009).

1.5 Challenges and opportunities of networks for forest system study and management

1.5.1 Node selection

The use of networks for forest systems understanding and eventually for forest management still requires work for the definition of nodes and connections based on spatial patterns. Considerable work is thus still needed to evaluate the importance of the identity of nodes regarding the conclusions drawn from the study of the structure of network.

The robustness of the approach could thus be questioned by evaluating the consistency of network indices with small variations in the identity of nodes or the definition of links. For example, landscape networks could be tested using different minimum sizes for the use of forest patches (thus increasing the number of nodes and possibly the connectivity of the network) or by varying the conditions for the existence of links (distance between patches, common species...). The variations in the resulting values of network indices (diameter, clustering coefficient...) could finally provide information about the consistency of networks regarding errors in the definition of nodes and links.

1.5.2 Function vs. identity?

Another issue in the integration of network thinking in forest ecology concerns the shift from a definition of objects based on their identity to a definition based on their function, hierarchical status or spatial position. Networks thus emphasize the function of objects in the systems rather than their identity.

Networks are therefore not initially designed o deal with questions regarding biodiversity or the role of rare species. As nodes generally represent groups of objects (species, patches, functional groups...) information regarding the diversity is mostly lost, although the abundances within each group could be integrated by varying the weight of the connections.

On the other hand, networks include no implicit hierarchy among nodes, a grouping according to species would tend to overestimate the functional role of rare species. A network could thus be constructed specifically to represent the functional role of certain species.

The focus of networks however remains the study of functional structure and should be considered a source of additional information regarding the complexity of systems, rather than a replacement for traditional measure of diversity. Especially since indices of species or functional diversity are already widespread and well understood and are in no particular need for replacement.

1.5.3 Studying dynamic systems with static representations?

The ultimate limitation of the application of networks in forest ecology lays in the fact that networks are inherently static whereas ecological systems are dynamic. Networks should therefore essentially be used as snapshots of forest states. However, different works, especially for the study of the fragility of networks (Albert, Jeong and Barabasi, 2000 ; Solé and Montoya, 2001 ; Montoya, Pimm and Solé, 2006), already studied the dynamic of the structure of networks by comparing several snapshots at different moment during the decay of the system. This approach relies on

specific indices representing the structure of networks (network diameter and connectivity) and could be adapted to reflect different dynamics. For example, the variation of classical indices of biodiversity (Simpson's or Shannon diversity indices, evenness, functional diversity...) could be measured on the communities represented by the network to observe the effects of variations in the structure of the network on diversity.

However, the major issue to the transposition of dynamic systems to networks is actually the variation of the role of forest objects in time (e.g. trees growing from seedlings under aerial competition to competitor trees with water limitations) that should translate as a variation in the identity of nodes or the definition of links. If the variations in the spatial patterns with time should reflect these variations and thus help adjust the construction of the networks to integrate the changes in roles and interactions, much research is still necessary to understand these transitions and properly model them.

1.5.4 Simple solution for the analysis of evident network systems

Despite the difficulties in the construction of networks and the identification of nodes, approaches inspired from networks can still be used in cases of systems when obvious spatial or hierarchical discontinuities exist. Hence, in some cases, the thorough sampling of spatial information can be partially avoided if some hypothesis about the clustering of interactions, the hierarchy of elements or spatial clustering can be exploited. For example, Kretzschmar et al. (2010) proposed that the hierarchy between elements (e.g. leaves distributed on the branches of different trees, or individual trees within different fragments of forest) or their proximity (individuals within the same spatial unit, elements along a path) could be used to replace the actual distances between individuals (in cases where the hierarchical or spatial co-occurrence are in fact more important than the actual distance between individuals, when distances cannot be measured or when the distance-range at which interactions occur is known with certainty or fixed by technical reasons). The patterns of

occupancy and abundance within the different levels of organisation in the community can then be measured through an embedded aggregation analysis to determine the complexity of the pattern through scales. If that method requires less data to be implemented, it however relies strongly on the relevance of the hypothesis about the structure of the community and should preferably be used in cases of undisputed hierarchical relations (epiphytes on tree-branches, nurse plants and their residents...) or obvious spatial or environmental segregations (bushes in savannah, rare species, altitudinal sub-communities...).

1.5.5 Integrating social and economic elements in ecological networks

Finally, a subject that is yet underexploited in the literature is the possibility offered by networks to integrate elements other than ecological and related to global societal issues from the social, economical and recreational spheres (Cumming *et al.*, 2010 ; Gonzalès and Parrott, 2012). The harvest pressure imposed by the forestry industry could for example be represented by links between commercial forest fragments in a forest network model the very same manner predation would be represented in a foodweb. Roads could also constitute links between elements allowing the connection between factories and forest plots. If the network is based on spatial patterns, then roads could also be directly involved in the emergence of bottleneck nodes as they tend to limit the circulation of some species and increase that of others (Hunter, 2002 ; Watkins *et al.*, 2003). The social relationships between different stakeholders competing for forest use (forest industries, environmentalists, native communities, etc.) could also be integrated in a network model of forest management (Bodin and Crona, 2009). For example, a given forest parcel may be highly praised by a native community or outdoor recreationalists (such as hikers or bird watchers). These cultural or recreational links could be added between the forest parcel node and these forest user groups. The addition of social links could transform a node into a hub and indicate the requirement for specific management.

Hence, in the context of network theory, elements of social, industrial and more generally human compartments could be integrated at the same hierarchical level as ecological processes and not only as top-down constraints (Cumming *et al.*, 2010). Notably, the application of network analysis to socio-ecological systems would allow us to determine the origins and impacts of hubs or bottleneck for the development and sustainability of each of the three objectives (ecological, social and economical) in ecosystem management (Michener *et al.*, 2001 ; Pickett, Cadenasso and Grove, 2005 ; Janssen *et al.*, 2006).

1.6 Conclusion

The main advantage of the integration of network theory and associated tools for forestry is that they fully acknowledge forest systems as being complex, dynamic and fully integrated. Network representations can also deal with various elements at different spatial and temporal scales and could bring a more systematic integrative approach to resource management. They permit an alternate understanding of the functional structure of systems. The framework of network could therefore allow us to focus management efforts on the most important or vulnerable elements (hubs, bottleneck, dead-ends) instead of developing generalist (and consequently inefficient) rules. In light of the increasing complexity of socio-ecological factors entering the management of any forest system and the rapidly changing conditions of our biological and physical world, such an approach is urgently required.

CHAPITRE II

HETEROGENEOUS FORESTS ARE NOT NECESSARILY COMPLEX: A COMPARISON BETWEEN MEASURES OF PATTERN COMPLEXITY AND TRADITIONAL STRUCTURAL INDICES

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2.1 Abstract

The maintenance of the diversity and complexity of forest structure and function is a growing concern for forest management. In the scientific literature, the diversity of species and structures are often closely related to complexity and thus complexity and heterogeneity are presented as correlates. This relationship is based on the definition of complexity as emerging from the multiplicity of objects in the system. However, complex patterns can emerge from relatively homogeneous systems and some very diverse ecological systems like tropical forests appear to produce random (and thus simple) patterns. Hence, the diversity of structures could be unrelated to the complexity of patterns. To test this hypothesis, we confront measures of structural heterogeneity obtained from the inventory of forest objects to a direct measure of the complexity of patterns using digital photos of the forest.

We compared five forest types in deciduous and mixed-wood forests following different natural and human-induced disturbances to test the effects of various stand structures on their complexity and structural heterogeneity. Secondary and maturing mixed-wood forests were sampled as well as deciduous forest plots to test the capacity of our indices of structural complexity and heterogeneity to differentiate between the effects of disturbances and species composition.

Each plot was mapped and all the trees were measured to allow the computing of different heterogeneity indices based on the biometric description of forest objects and species diversity. The plots were also photographed in order to compute of a set of indices (Mean Information Gain: MIG) measuring the complexity of the patterns emerging from the distribution of forest objects. Our two sets of indices (heterogeneity indices and MIG) were then compared using multivariate analysis (principal component analysis and redundancy analysis).

The results of the MIG indicate that our measures of the complexity of patterns separate disturbed and undisturbed stands as well as mixed-wood and deciduous forest plots. Disturbances tend to create more complex patterns in forest stands. Our results also indicate that most structural indices are negatively correlated to MIG complexity indices.

This work also informs us about emerging patterns of light and perspectives that can not be captured by traditional sampling of forest structures. These emerging patterns could become valuable new indicators for the understanding of habitats used by wildlife and the effects of natural and man-made disturbances on patterns within forest stands.

Keywords: Complexity, Digital photographs, Heterogeneity, Forest structure, Patterns, Light.

2.2 Introduction

The word 'complex' is often used by forest ecologists as a buzzword to describe the overall impression given by diverse, irregular or heterogeneous forest ecosystems (Lindenmayer *et al.*, 2000 ; Zenner and Hibbs, 2000 ; Franklin and Van Pelt, 2004). In the literature, forest dynamic is often qualified as 'complex' to refer to unpredictable processes and responses to disturbances. Structures and patterns are also often labelled 'complex' to describe disorder in the spatial organisation of objects. Complexity is also often discussed in an effort to emphasize the intricacy of ecological and anthropogenic systems and to underline the fact that the description of individual systems or single processes is not sufficient to understand the whole system (Pickett, Cadenasso and Grove, 2005 ; Liu *et al.*, 2007). 'Complex' is therefore used as an umbrella descriptor to emphasize the overall interest of a system and justify its study and conservation as a whole rather than as an addition of functions (Goldstein, 1999).

Spatial patterns in forest are the visible result of a complex history of processes and disturbances occurring at different scales (migration, selection, interactions, reproduction, mortality, cuts, fire...) and as such they constitute natural subjects for the study of complexity. In forest ecology, spatial patterns and the spatial distribution of individuals (point patterns) have long been used to infer the processes that induced them (seed dispersal (Pastor, Cohen and Moen, 1999), biotic interactions (Wiegand *et al.*, 2007 ; Boivin *et al.*, 2010), species diversity (McArthur, 1972 ; Hubbell, 2001), gap (Solé and Manrubia, 1995), and fire or pest propagation (Muzy *et al.*, 2005 ; Pérez and Dragicevic, 2010)).

The study of spatial patterns often requires separating forest systems into compartments and therefore studying the spatial distribution of vegetation, wildlife, understorey plants or dead-wood separately, each compartment being a potential habitat for another group (dead-wood for insects or fungi, the canopy for birds, the

understorey for small mammals, landscapes for tree species...) (McElhinny *et al.*, 2005).

Within each compartment of the system, patterns are then defined as the sum of individual forest objects (trees, understorey plants, gaps, forest patches), and characterised as a combination of (a) an inventory of forest objects over a specific surface (DBH distribution, number of vegetation layers, species composition, species richness) reflecting the biodiversity of the site, (b) a quantification of the variability of forest objects in size and shape (standard error or variances, Shannon diversity) and (c) a set of statistics describing the spatial distribution or the covariance of each type of object (or only of the most important objects) (Ripley's K, Moran's I, Pielou...) (see Lähde *et al.*, 1999 ; Zenner and Hibbs, 2000 ; Neumann and Starlinger, 2001 ; Staudhammer and LeMay, 2001 ; McElhinny *et al.*, 2005 for reviews and examples).

The resulting spatial patterns can then be considered complex depending on the values for each of these descriptors. Commonly, complex habitats are described as (a) diverse, (b) variable and (c) disordered. The different indices of structural heterogeneity that are employed to describe forest patterns at the stand level thus entail an implicit gradient of complexity from heavily-managed forests to natural forests and from young to old-growth forests (as vegetation layering, species diversity and disorder in the spatial distribution tend to increase with age and naturalness). This gradient accompanies the common idea that the overall biodiversity (of both species and functions) is higher in old-unmanaged forests than in young forests or plantations. It also implies that the most complex dynamics occur as forests age (Franklin and Van Pelt, 2004 ; Ishii, Tanabe and Hiura, 2004 ; Zenner, 2004).

This assumption about the relation between ageing and complexity is generally supported by earlier (more abstract) research on complexity. The sand-pile experiment for example showed that complex temporal patterns following catastrophes (in this example, avalanches) could emerge from perfectly homogeneous

and regular systems (Bak, Tang and Wiesenfeld, 1987 ; Yoshioka, 2003). The relationship between forest ageing and increase in complexity has also been formalised in the form of forest successions where the structure diversifies with the introduction of gap dynamics in old forests. Hence, old and natural forests are expected to be more complex than young disturbed forests; higher complexity should allow more original spatial associations in the patterns and thus allow more original processes to emerge, therefore promoting a greater adaptability and resilience.

However, the understanding of the relationship between diversity, disturbances, heterogeneity and the overall complexity of forest systems still relies on hypothesis and theories. The testing of these hypotheses requires the development of tools that allows measuring the complexity of patterns directly.

To represent complexity, we chose an index, the Mean Information Gain (MIG) that allows measuring the disorder of patterns. This index actually measures the diversity of associations between the pixels in digital photographs of forests and represents the complexity of the patterns created by the mixing between forest objects (trees, dead trees, stumps, understorey plants...) of different size, shape and species.

Our research applies the MIG (Proulx and Parrott, 2008) to forest systems and to compare this index to more traditional measures of diversity and heterogeneity and to indicators of disturbances. This confrontation between indices of complexity and of heterogeneity, diversity and indicators of disturbances could finally allow us to test a set of hypotheses and or at least to discuss how diversity, heterogeneity and disturbance regimes could influence the complexity of forest patterns.

Based on the literature, we hypothesized that:

(1) Forest stands with heterogeneous layers of vegetation and high species diversity have more complex forest pattern.

(2) As a corollary, forest stands with very dense and homogeneous layers (e.g. dense fir regeneration) have less complex forest pattern.

Our primary goal is to compare whether the MIG for the patterns of vertical distribution of vegetation provides the same ranking of forests (for stands with different compositions or having undergone different disturbances) than the traditional measures of forest structural diversity and heterogeneity.

2.3 Methods

2.3.1 Study areas

Fifteen 40x40 m forest plots with different natural and man-made disturbance histories were sampled. Twelve forest plots are located in the mixed wood-forest near La Tuque (47° 26′ 00″ N, 72° 47′ 00″ W) in central Quebec and three additional plots in the deciduous forest in southern Quebec at Mount St-Hilaire (45° 34′ 00″ N, 73° 12′ 00″ W).

The three deciduous forest plots (DF) at Mount St-Hilaire are in a sugar maple (*Acer saccharum*) dominated forest in a xeric environment and were heavily disturbed by deer grazing which resulted in the complete absence of an understorey stratum.

The mixed-wood forests are dominated by balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), red maple (*Acer rubrum*) and yellow birch (*Betula alleghaniensis*). However the composition varies depending on the histories of sites (red maple and trembling aspen are predominant in secondary forests and one of the mature forest plots has large mono-specific patches of balsam fir). We sampled four different forest histories. All sampled forest stands originated from a major fire in 1923. Mature forests (MF) were left untouched, secondary forests (SF) were clear-cut during the 1970's and are untouched since. Partial-cut treatments (PC50 and PC35) were both partially harvested during the winter of 2007-08 (see Table 2.1 for an overview of the history of the forest treatments).

Both partially cut forests were harvested with the same basic technique. A 5 m wide temporary track was clear-cut, and from that track two 7 m wide strips are thinned to ~50% of their basal areas. Between these harvested strips retentions areas of respectively 5 m and 19 m for PC50 and PC35 were left uncut in order to attain a total 50% or 35% basal area removal (see Figure 2.1 for an illustration and explanation of the harvest design).

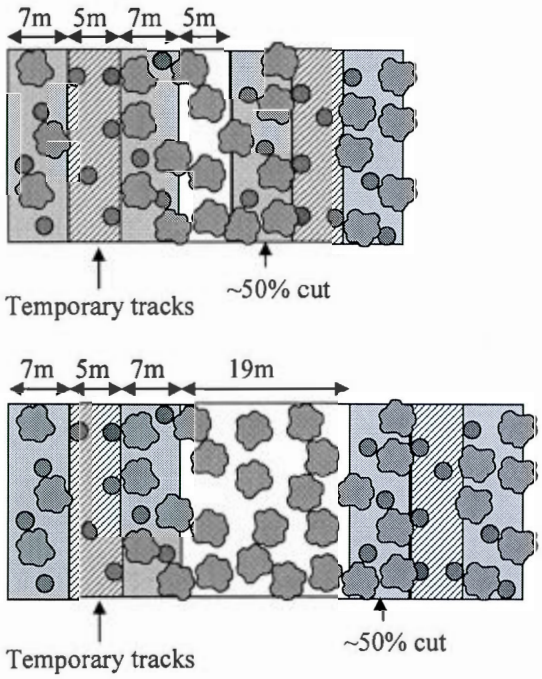


Figure 2.1 Harvest designs for partial cut with (a) 50% basal area removal (PC50%) and (b) 35% removal (PC35%). Partial cuts are made around temporary clear-cut tracks (hatched bands). On each side of these tracks, the largest tree of each 3 trees is harvested in two 7 meter wide interbands (grey bands). The two different harvest intensities are achieved by varying the width of the retention bands (white bands). In PC50% the retention band is 5 meters wide (a) and in PC35% it is 19 meters (b).

Table 2.1 Natural and man-made disturbance histories of the different study sites

Mature Forests (MF)	Secondary Forests (SF)	Partial Cuts 35% (PC35%)	Partial Cuts 50% (PC50%)	Deciduous Forests (DF)
1923 Fire				
Some low level selective cuts	1970's Clear cuts			Deer grazing
		2007 partial cut (35% basal area)	2007 partial cut (50% basal area)	

2.3.2 Sampling design

The forest plots were sampled in July and August 2008 (PC50% and PC35%), 2009 (SF and MF) and 2010 (DF). In each of the five treatments, we photographed and inventoried three 40x40 m replicate plots.

Each forest plot was divided into 16 subplots (10x10 m) that were mapped and photographed. All living trees above 10 cm in diameter at breast height (DBH) were mapped, identified to the species and measured (DBH, diameter at breast height, basal diameter, crown dimensions in 2 orthogonal directions, height of the lowest living branch).

Table 2.2 Camera settings (see Proulx and Parrott, 2008 for more explanation about the choices behind these settings)

Camera	Canon EOS Rebel XTI 400D
Focal length	18 mm
Aperture diameter	6.3 mm
Focus distance	10 m
Tripod's head above ground	1.3 m
Depth of field (DF)	2 m - infinity
Exposure mode	Aperture priority
Time window for shooting	7h00-16h00
Visual obstruction < DF	Avoided
White balance mode	Natural light
Resolution	1288 x 1936 pixels

Each 10x10 m subplot was also photographed from two perpendicular points of view (Figure 2.2) under uniformly overcast skies to normalise light conditions. The camera was set up horizontally on a tripod with the objective 1.3 m above the ground, thereby capturing the layering of vegetation in the mid-forest strata, the understorey and depending on vegetation crowding, the lower layers of the canopy (see Table 2.2 for photographic settings, Figure 2.2 for camera positioning and Figure 2.3 for examples of pictures).

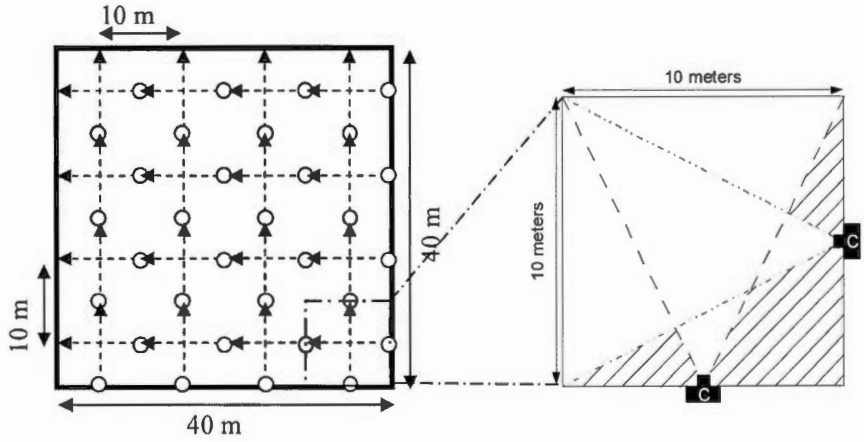


Figure 2.2 Left: Map of the 40x40 meter quadrates divided into 16 10x10 meters subplots. Camera positions are shown as open circles and the directions of the photographs as dashed arrows. Right: Schematic representation of photographic sampling in 10x10 m plots. Hatching represents dead angles of the photos.

2.3.3 Measuring the complexity of forest patterns in photographs

In this work we tested a method that directly measures the complexity of patterns in photographs. Digital photographs allow the exhaustive sampling of the visible vegetation layer and the index we chose, the Mean Information Gain (MIG) measures the disorder in the spatial associations of pixels in the photos. As the pixels of the photographs represent the actual forest objects and their spatial distribution, the measure of the complexity of pixel patterns actually constitutes an indicator of the

complexity of forest patterns (Andrienko, Brilliantov and Kurths, 2000 ; Proulx and Parrott, 2008).

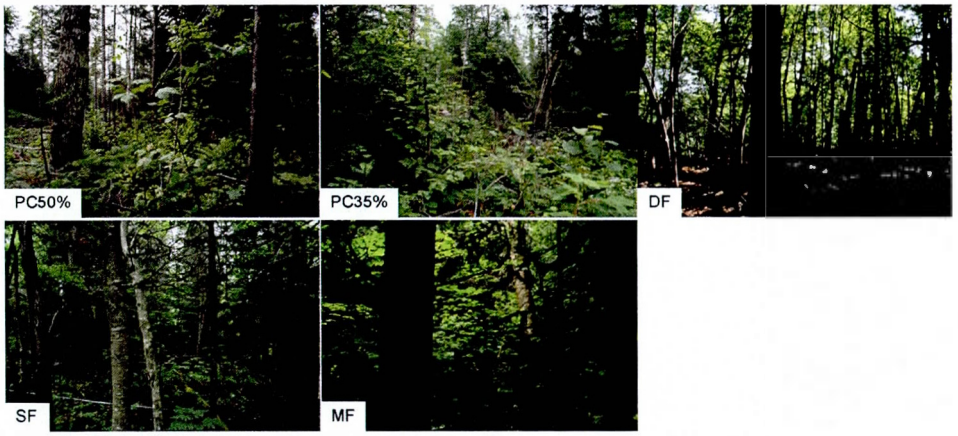


Figure 2.3 Example of photos taken in each forest type.

2.3.3.1 Computing

The photographs were first converted from RGB (the original coding of colours in the jpeg images created by our camera) to HSB (Smith, 1978). As the values of pixels in HSB images are continuous and may therefore be unique, the values are then clustered into 10 classes for each band (H, S, B) of the image (Proulx and Parrott, 2008). The complexities of the patterns of pixel values in the resulting 3 matrices are then computed separately in MATLAB (V 7.6, 2008).

The complexity of each matrix is quantified through the measure of its information content with a Mean Information Gain (MIG) index. The MIG produces an estimate of the length of the description of a pattern. The length of the pattern increases with the unpredictability of the pattern, and thus the MIG increases from 0 for completely ordered patterns to 1 for completely random patterns. The most complex patterns, which integrate both deterministic and random features, are represented by intermediate values of MIG (~0.55) (see Figure 2.4).

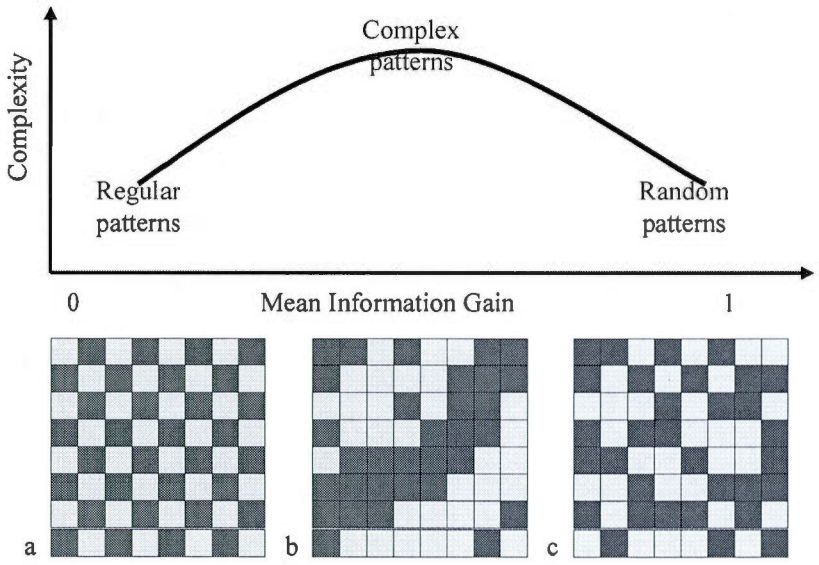


Figure 2.4 Convex relationship between Mean Information Gain (measure of complexity based on the length of the description of the pattern) and the complexity of spatial patterns. a) regular pattern, b) complex pattern, c) random pattern.

The MIG is computed on the three bands of the photos (Hue-Saturation-Brightness) using equation (2.1) (Proulx and Parrott, 2008):

$$MIG = \frac{H[\chi] - H[\gamma]}{\log N^4 - \log N^1} \qquad \text{Eq. 2.1}$$

where N is the number of clusters of possible values for each pixel (N = 10) and N^4 is the number of theoretical 2x2 combinations of pixel values, $H[\chi]$ is the joint entropy among 4 neighbouring pixels (see equation 2.2), and $H[\gamma]$ the marginal entropy of pixel values in the image (Eq. 2.3).

$$H[\chi] = - \sum_{i=1}^{N^4} p(\chi\iota) \log p(\chi i) \qquad \text{Eq. 2.2}$$

$p(\chi i)$ is the empirical frequency of observations for a specific 2x2 spatial association of pixel values χi in the image.

$$H[\gamma] = - \sum_{i=1}^{N} p(\gamma\iota) \log p(\gamma i) \qquad \text{Eq. 2.3}$$

$p(\gamma i)$ is the frequency of observations for a pixel value independent of its location in the image.

The resulting complexity values for each band are then averaged between the two photos taken for each 10x10 m subplot, resulting in a combination of 3 values of complexity (one for each band of the HSB image) to describe each subplot.

Additionally, Mean Mutual Information (MMI) was also calculated on the matrices for the three bands (HSV) of the photographs in order to identify the maximum complexity value of the MIG. MMI is the opposite of MIG in the sense that it measures the amount of order in patterns and reaches its highest values (MMI = I) for completely uniform patterns. MMI was calculated with the following equation (2.4):

$$MMI = \frac{4H[\gamma] - H[\chi]}{4\log N^1 - \log N^1} \qquad \text{Eq. 2.4}$$

where $H[\chi]$ and $H[\gamma]$ are calculated as in equations 2.2 and 2.3, and N the number of classes in each band (N = 10).

The value corresponding to the maximum complexity of the MIG is determined as the point of inflexion of the relation between MIG and the MMI x MIG (Proulx and Parrott, 2008).

In this case, the MIG value corresponding to the highest possible complexity is 0.55 according to the point of inflexion for the relationship between MIG and MIG x MMI (Figure 2.5).

All values for MIG in the three bands were distributed between 0.05 and 0.64. Our results therefore indicate that the patterns in the photos range from order to complexity. In our forests increasing scores of MIG can thus be directly interpreted as increases from ordered to complex patterns.

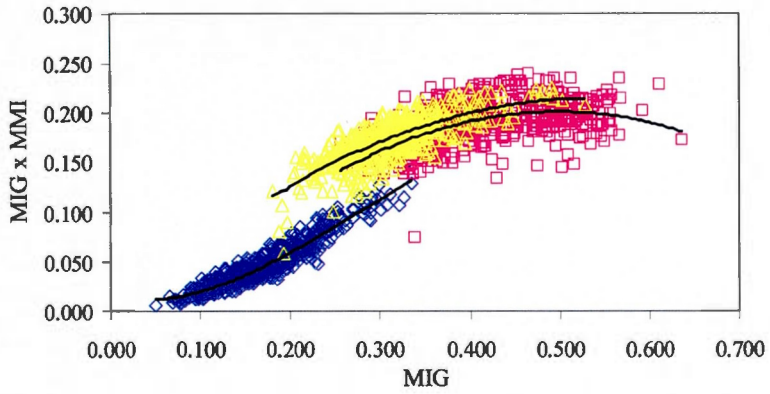


Figure 2.5 MIGxMMI as a function of MIG. Blue diamonds: Hue (R^2=0.89). Pink squares: Saturation (R^2=0.34) and Yellow Brightness (R^2=0.59). The MIG value corresponding to the maximal complexity of patterns is 0.55.

2.3.4 Forest heterogeneity and diversity based on object mapping

2.3.4.1 Canopy closure

The sample plots that were used for the MIG photographs were also used to photograph the canopy of each 10x10 m subplot from two angles (see Figure 2.2 right). Each photograph was individually converted to black and white in order to allow the distinction between the sky and the vegetation. The closure of the canopy for each image is defined as the percentage of black pixels in the image. The final canopy closure value for each 10x10 m subplot is the average of canopy closure calculated from the two photos.

Table 2.3 Structural and diversity indices computed from mapping the forests

Abbreviated names	Computing	Description
Canopy	% of black pixels in canopy photographs	Estimate of canopy closure measured on photos.
Luminance	$L = \frac{1}{\log(\text{Shutter speed})}$	Estimate of incoming light in the mid-layer photographs.
Simpson	$D = 1 - \sum_{i=1}^{s} p_i^2$	Simpson's diversity index of tree species. p_i is the proportion of basal area for species i.
USSpRich	Species richness of understorey species.	
USCover	Percent cover of understorey vegetation.	
Coniferous	$\%Con = \frac{Con}{Con + Dec}$	Proportion of coniferous trees in the subplot. Con: The number of individuals from coniferous species (balsam fir, white and black spruce, white, red and grey pine) Dec: The number of individuals from deciduous species
TreeNb	Number of living trees in the 10x10 m plots.	
MeanDBH	Average of living tree DBH in cm.	
ShanDBH	$H' = - \sum_{i=1}^{n} p_i \ln p_i$	Shannon diversity of trees among 5 cm DBH classes. p_i is the proportion of individuals in the class i of DBH.
SCIh	$SCI = \frac{SCI^*}{A_T}$	Structural Complexity Index (SCI) measured for the heights of the lowest living branches of trees (Zenner and Hibbs, 2000). SCI* is the sum of the surface areas of the triangulated network between the lower branches of each tree. A_T is the ground area covered by trees.

2.3.4.2 Indices of heterogeneity and diversity from the mapping

Several indices were computed from the forest plot maps in order to describe the different dimensions of diversity and structure of the plots, the references of each index and a short explanation of how they are computed are listed in Table 2.3 All indices were computed in R (R Development Core Team, 2010) (packages: vegan (Oksanen *et al.*, 2011), ade4 (Dray and Dufour, 2007), spatstat (Baddeley and Turner, 2005), rimage (Nikon Systems Inc., 2010), adehabitat (Calenge, 2006)).

Among these indices, the closure of the canopy and the estimate of luminance are both computed using data from the photographs taken in the subplots (see previous paragraph "Canopy closure"). As the camera was set on aperture priority, the speed of the camera shutter is directly related to the amount of light available in the mid-forest layer and therefore constitutes a good representation of luminance. Luminance was thus estimated as the inverse of the log-linearized shutter speed for each MIG photograph and then averaged between the two photos taken in each subplot.

Species diversity of the forest plots was calculated using Simpson's index of diversity for trees and by species richness for the understorey community. The understorey vegetation was inventoried for species richness and its percent cover was visually estimated in the subplots.

The proportion of coniferous species (balsam fir, white and black spruce) in each subplot was also computed to account for mixing of deciduous and coniferous trees in mixed-wood forest plots. Considering the shape of coniferous trees this index is also a descriptor of the amount of dense vegetation in the lowest layers of the vegetation.

The tree community is described by the density of living trees, their mean diameter at breast height (DBH) and by Shannon's diversity for the distribution of trees in 5 cm DBH classes. The Shannon diversity for DBH classes gives an indication of the mixing between tree sizes in each subplot and thus the heterogeneity of the tree layer.

The Structural Complexity Index (SCI) is another index that is used to represent the layering of the vegetation (Zenner and Hibbs, 2000). SCI measures the irregularity of the surface created by the lowest layer of living tree branches and thus represents the heterogeneity of vegetation layers.

2.3.5 Statistical methods

Multivariate analyses were chosen for the evaluation of the relationships between the different indices of heterogeneity diversity and complexity. These tests allow for the simultaneous observation of all indices and their correlations. All indices were normalised prior to the analyses in order to bring them to a normal distribution and allow for the use of parametric statistics.

We tested the spatial autocorrelation between MIG values in order to verify if the 10 x 10 subplots could be used as individuals. The details of the test are described in Appendix 2.1 and the results in Appendix 2.2. Considering these results, we considered that the MIG values were sufficiently independent to be used individually in the RDA and PCA.

2.3.5.1 Principal Component Analysis (PCA)

Two principal component analyses were executed on the matrix of the heterogeneity and diversity indices from forest mapping and on the MIG indices using R (packages: vegan, ade4) . These analyses were computed in order to observe the main structural differences between forest types and their distribution when described by the MIG indices. All the PCs with eigenvalues superior to 0.15 are interpreted in our results.

Moreover, circles of equilibrium contribution (CEC) were used to identify the variables with the highest contributions to the distribution of subplots. These circles are defined by a radius of $r = \sqrt{(d/p)}$ with d as the number of axes represented in the plot (d = 2) and p the number of variables (p = 10 for PCA on heterogeneity and diversity indices and p = 3 for the PCA on MIG indices). The variables with vectors

longer than this radius can be considered to have a stronger contribution to the distribution (Borcard, 2011).

2.3.5.2 Redundancy Analysis (RDA)

We also conducted a redundancy analysis (RDA) that is intended to evaluate the relationship between structural indices from the mapping and MIG complexity indices. The structural indices are used as explanatory variables for the MIG indices (response variables) (Legendre and Gallagher, 2001).

Permutation tests were computed to test for the significance of axes and explanatory variables; only the axis and variables that had a larger contribution to the analysis than 90% of the permutation are interpreted (Borcard, 2011).

2.4 Results

2.4.1 How structural heterogeneity and diversity represent different forests

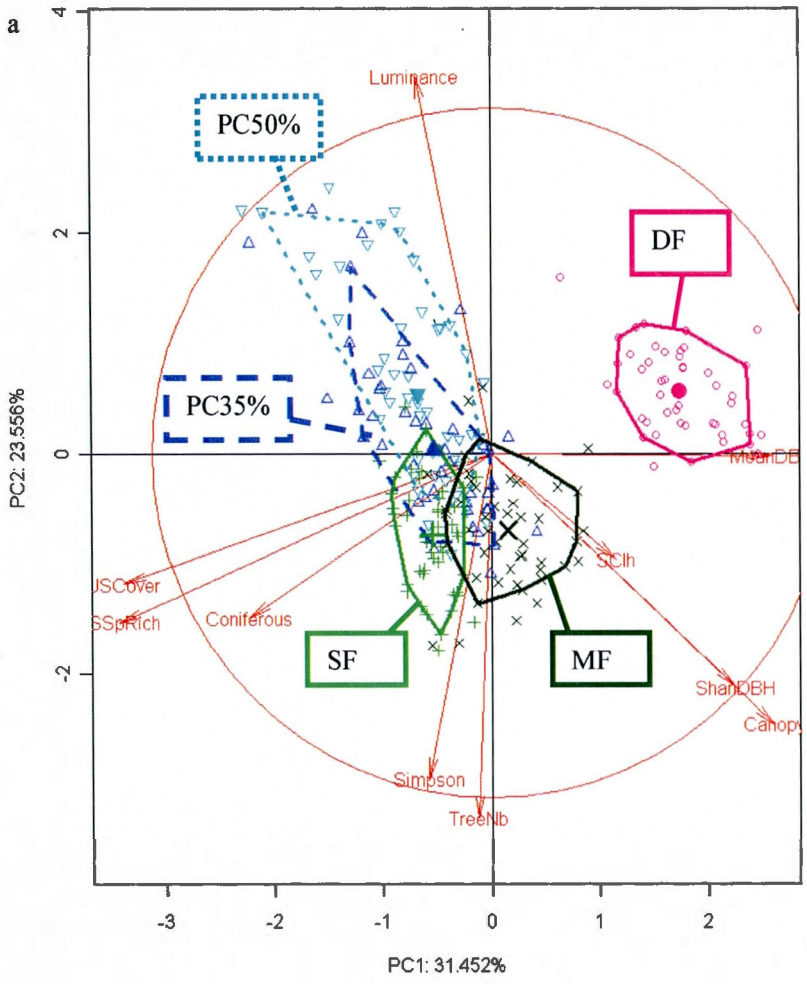
The circle of equilibrium contribution (CEC) (Figure 2.6.a) indicates that most variables make a stronger contribution to the analysis than average, with the exception of the SCI on branch heights which represents the heterogeneity of tree layering ('SCIh'), the mean DBH of trees ('MeanDBH') and the proportion of coniferous species in the subplots ('Coniferous').

The PCA (Figure 2.6.a) of structural and diversity indices reveals a clear separation along the first axis between the mixed-wood and deciduous forests. This distinction is mainly mediated by indices related to the understorey richness and cover and to the presence of coniferous species ('USSpRich', 'USCover' and 'Coniferous'). Deciduous forests (DF) are also characterised by higher mean DBH although this descriptor makes a weak contribution to the projection.

The structural distinction between deciduous forests and mixed-wood plots is mainly based on the absence of an understorey in deciduous plots (low 'USSpRich' and 'USCover'). Another interesting feature of deciduous forests is that they have

both closed canopies (high 'Canopy') and relatively high luminance (Luminance), which indicates a high permeability of the canopy to light (Figure 2.6.b).

All mixed-wood forest subplots are more aggregated along the first axis of the PCA. However, a differentiation along the second axis appears between partially-cut forests and closed-forest. Obviously, partial-cuts are not as dense (low 'TreeNb'), have more open canopies (low 'Canopy' scores) and therefore higher luminance. Closed forests (MF and SF) have more diverse distributions of trees among DBH classes ('ShanDBH') and more heterogeneous vegetation layers (higher 'SCIh' scores). Mature forests have larger trees than secondary forests as demonstrated by their distribution along the first axis. It is also noteworthy that the points belonging to partial cuts (PC35% and PC50%) are more scattered and partially overlap the subplots from closed-forests.


a
Luminance
PC50%
DF
PC35%
MeanDB
SCIh
USCover
SSpRich
Coniferous
SF
MF
ShanDBH
Canopy
Simpson
TreeNb
PC2: 23.556%
PC1: 31.452%
4
2
0
-2
-3
-2
-1
0
1
2

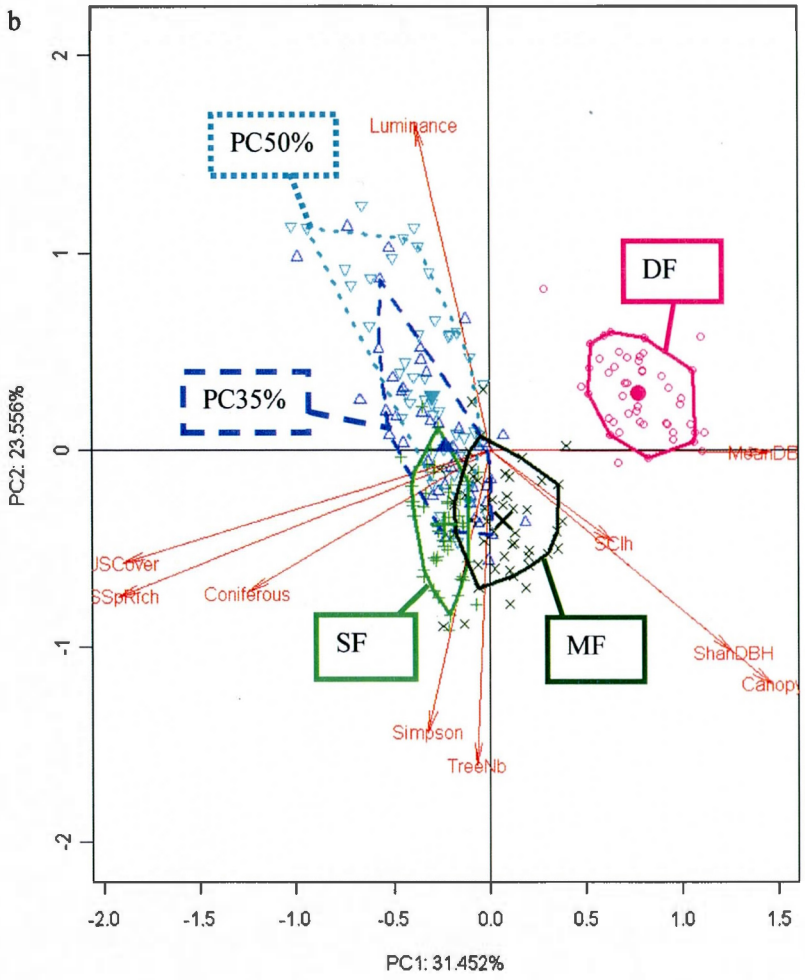
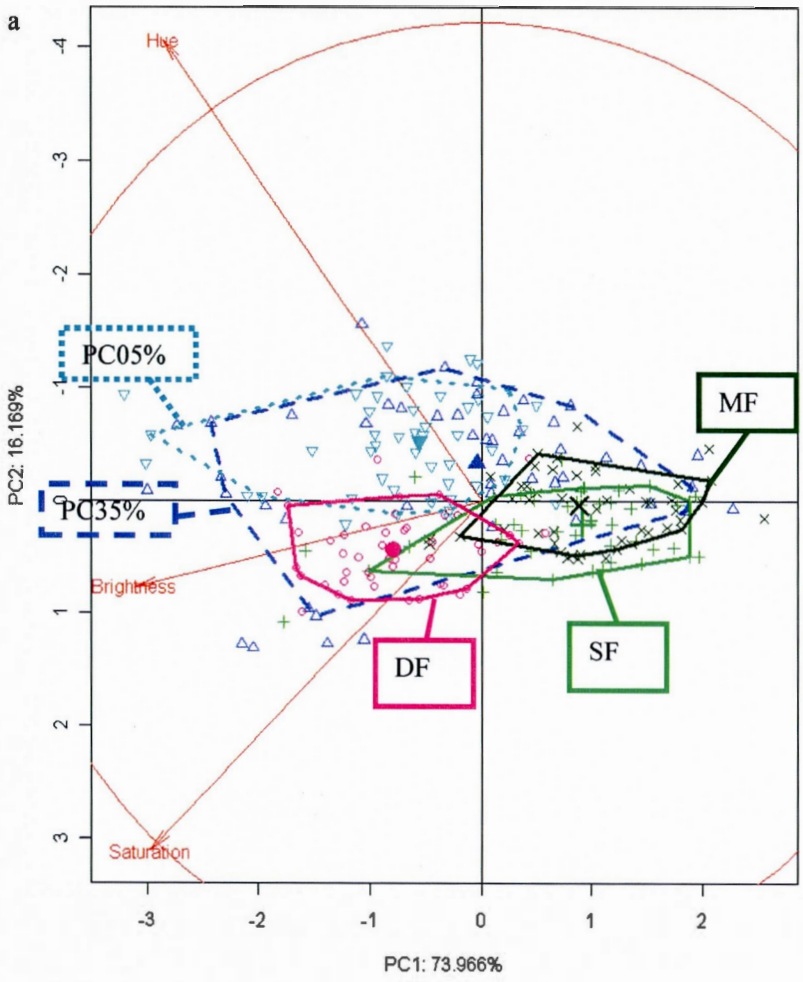


Figure 2.6 Biplot of the first two PCA axes of heterogeneity indicators (red arrows) as data descriptors. (a): Distance biplot, the red circle represents CEC; the distances between objects represent their distances in the multidimensional space. The projection of the sites was magnified (x4) for readability. (b): Correlation biplot, the angles between vectors represent their correlations. Envelops highlight the distribution of 90% of the points for each treatment, solid symbols represent the median of each group: Turquoise ▼ and dotted line: 50% Partial cuts, Blue ▲ and dashed line: 35% Partial cuts, Light green + and solid line: Secondary forests, Dark green x and solid line: Mature forests, Pink ● and solid line: Deciduous forests.

2.4.2 How MIG sees forests

In the PCA, the vector of MIG on Brightness patterns is shorter than the radius of the CEC (Figure 2.7.a). This indicates that the different forest plots are differentiated more by the patterns in Hue and Saturation values than by Brightness.

The distribution of subplots in the PCA (Figure 2.7.a) shows a remarkable grouping of the photos according to their original forest types, indicating similarities between the patterns photographed in each forest type. A clear separation appears along the first axis between photos taken in mature mixed-wood forests (MF) which exhibit low complexity for all three bands, and those from deciduous forests (DF) with higher complexity values for Saturation and Brightness. Mature mixed-wood forests (MF) and secondary forests (SF) completely overlap along the two first axes indicating no clear differences in the complexity of their vertical patterns. Similarly, partial-cuts (PC50% and PC35%) overlap, although pictures from the PC35% plots cover a wider range of complexity values on all three bands (Hue, Saturation and Brightness). The range of values of MIG for the three bands is wider in both partial-cuts than in closed-forests in general (DF, SF or MF) (Figure 2.7.b). PC50% plots are distinctly separated from closed-forests by higher complexities in Hue, whereas the subplots from the PC35% are scattered across all the other groups, indicating similarities in the complexity of their patterns with all of the other forest types.


a
Hue
PC05%
PC35%
MF
DF
SF
Brightness
Saturation
PC2: 16.169%
PC1: 73.966%
-4
-3
-2
-1
0
1
2
3

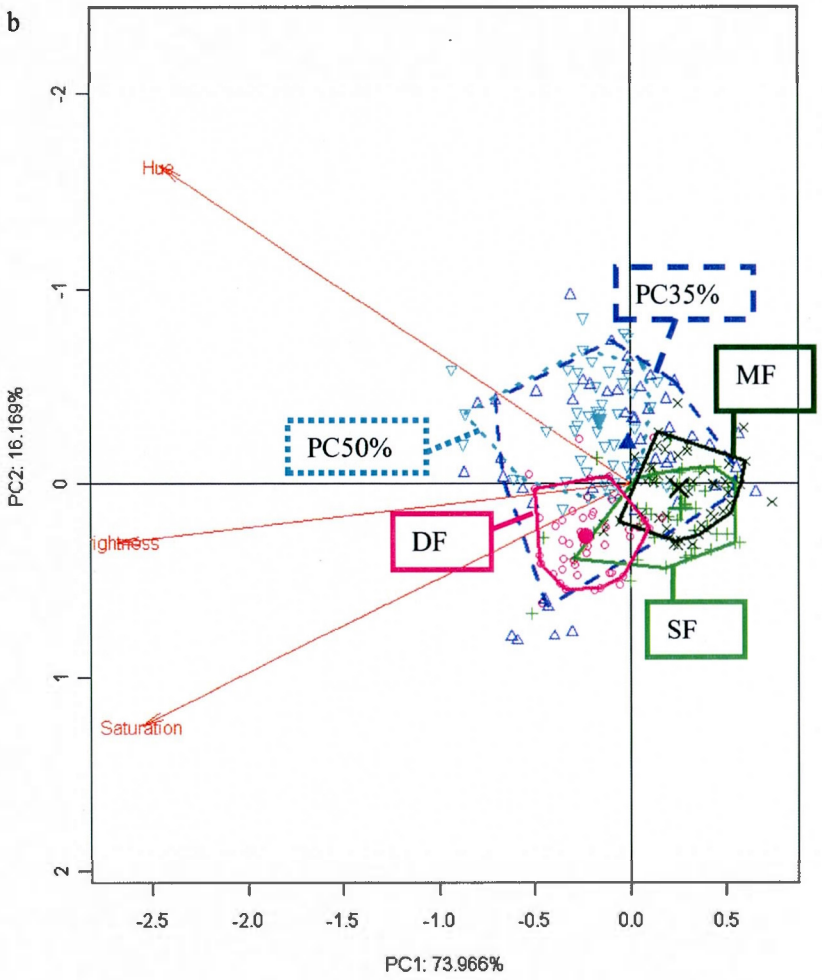


Figure 2.7 Biplot of the first two PCA axes of MIG complexity indices (red arrows) as data descriptors. (a): Distance biplot, red circle represents CEC; the distances between objects represent their distances in the multidimensional space. The projection of the sites was magnified (x4) for readability. (b): Correlation biplot, the angles between vectors represent their correlations. Envelops highlight the distribution of 90% of the points for each treatment, solid symbols represent the median of each group: Turquoise ▼ and dotted line: 50% Partial cuts, Blue ▲ and dashed line: 35% Partial cuts, Light green + and solid line: Secondary forests, Dark green x and solid line: Mature forests, Pink ● and solid line: Deciduous forests.

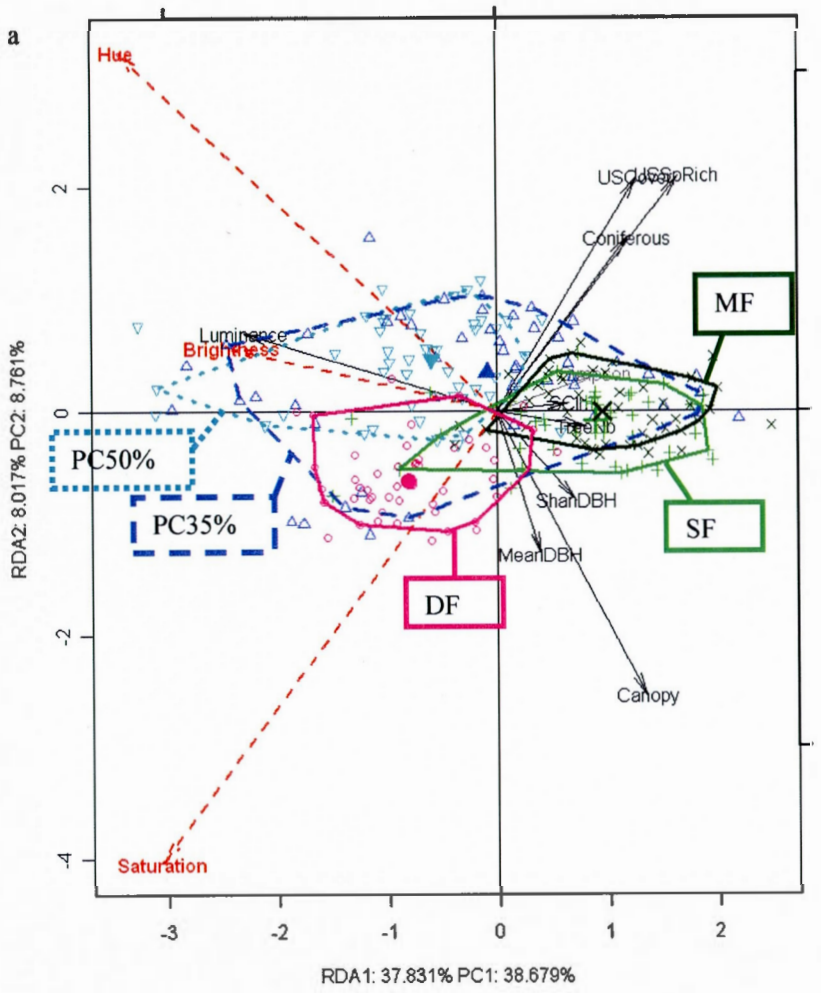
2.4.3 Confrontation between MIG indices and traditional heterogeneity and diversity indices

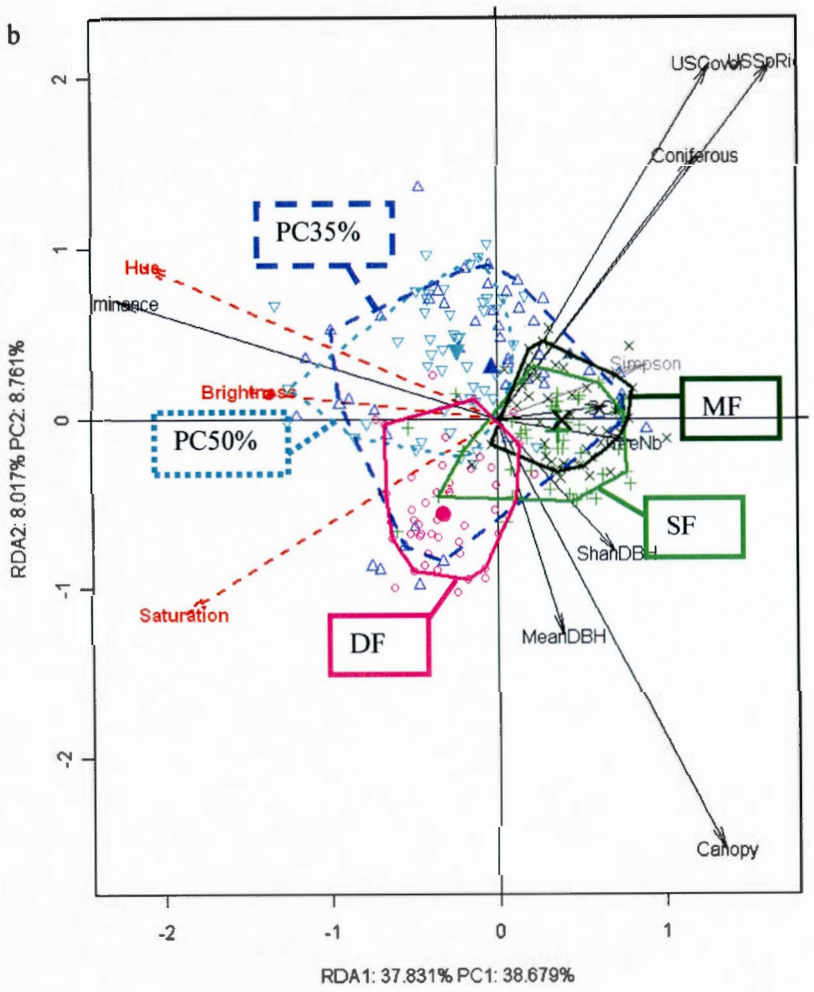
The three axes of the RDA are significant (Table 2.4) and the distribution of plots and descriptors may therefore be interpreted with confidence along the three axes. All heterogeneity and diversity indices are also significant, except for the Simpson diversity index (see Table 2.5 for the results of permutation tests), which can therefore not be used in the interpretations (Figure 2.8.a).

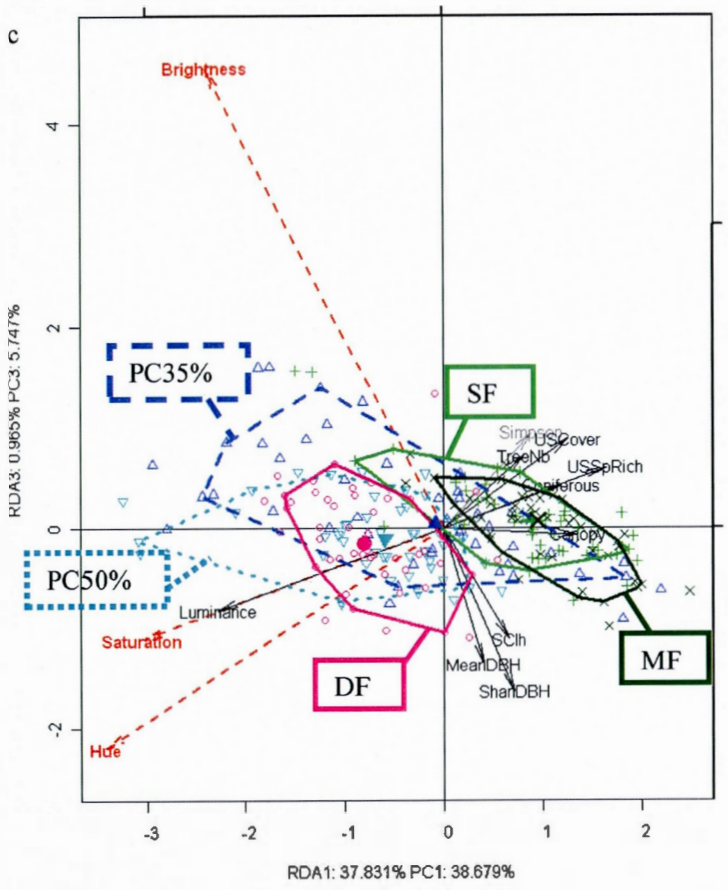
The first observation regarding the confrontation between MIG values and traditional heterogeneity and diversity indices is that these two sets of indices are generally negatively correlated (see RDA Figure 2.8.b). Indices related to species diversity ('USSpRich' and 'Coniferous') are directly opposed to the complexity of Saturation patterns and indices of tree density ('TreeNb'), the heterogeneity of tree DBH ('ShanDBH') and the heterogeneity of vegetation layers ('SCIh') are negatively related to the complexity of Brightness and Hue patterns.

In essence, forest plots with closed-canopies (high scores of 'Canopy'), diverse understorey ('USSpRich') and a high proportion of coniferous species ('Coniferous') and which therefore have more layers of vegetation, have lower indices of complexity of patterns than plots with low diversity, even-aged trees and more open canopies. These results are in direct opposition with the general hypothesis that heterogeneity and biodiversity increase the complexity of spatial patterns.

The complexity of patterns created by the distribution of Brightness values in the photographs (hereafter referred to as 'Brightness patterns') is negatively correlated with canopy openness; however the heterogeneity of vegetation layers ('SCIh') does not contribute to increase the complexity. As a consequence, the maximum complexity of Brightness patterns is achieved in the least dense plots (low 'TreeNb') with open canopies and maximum luminance, found in the PC50% plots.


a
Hue
Luminance
Brightness
Saturation
USCDSSpRich
Coniferous
MF
SF
DF
PC50%
PC35%
ShanDBH
MeanDBH
Canopy
RDA2: 8.017% PC2: 8.761%
RDA1: 37.831% PC1: 38.679%
2
0
-2
-4
-3
-2
-1
0
1
2


b
USCover
USSpRi
Coniferous
PC35%
Hue
minance
Brightness
PC50%
Simpson
MF
TreeNb
SF
ShanDBH
Saturation
DF
MeanDBH
Canopy
RDA2: 8.017% PC2: 8.761%
RDA1: 37.831% PC1: 38.679%
2
1
0
-1
-2
-2
-1
0
1


c
Brightness
PC35%
SF
PC50%
Luminance
Saturation
DF
MF
Hue
USCover
TreeNb
USSpRich
Canopy
SCIh
MeanDBH
ShanDBH
RDA3: 0.965% PC3: 5.747%
RDA1: 37.831% PC1: 38.679%

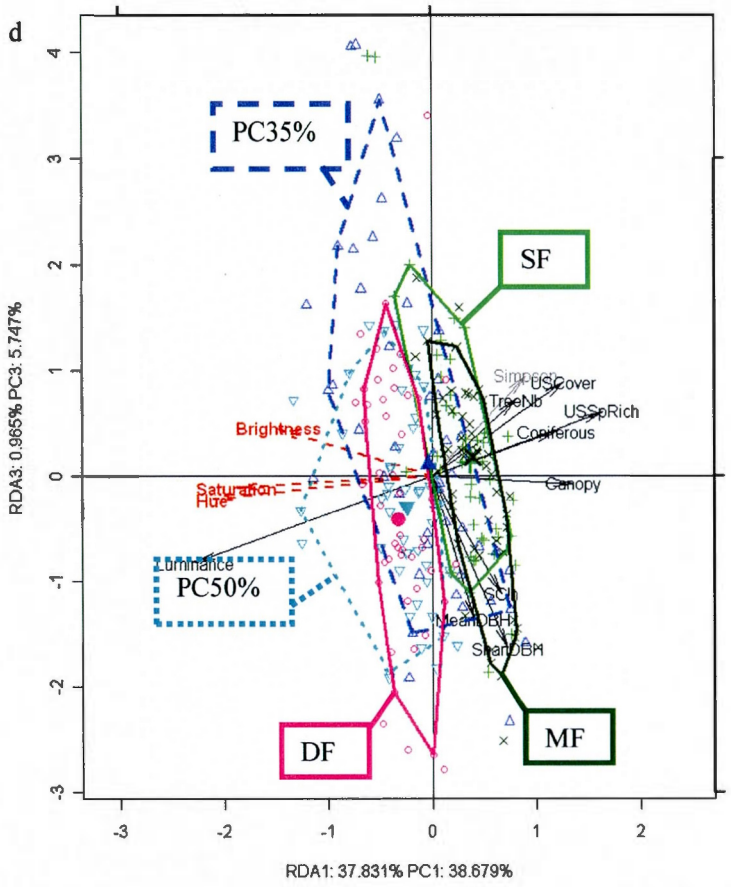


Figure 2.8 RDA of MIG complexity indices (red dashed arrows) as data descriptors and heterogeneity indicators (black arrows) as explanatory variables, the length of the vectors of explanatory variables was magnified (x3) for readability. (a) and (b) are the biplot projections for axes 1x2, (c) and (d) for axes 1x3. (a) and (c): Distance biplot, the distances between objects represent their distances in the multidimensional space. The projection of the sites was magnified (x4) for readability. (b) and (d): Correlation biplot, the angles between vectors represent their correlations. Envelops highlight the distribution of 90% of the points for each treatment, solid symbols represent the median of each group: Turquoise ▼ and dotted line: 50% Partial cuts, Blue ▲ and dashed line: 35% Partial cuts, Light green + and solid line: Secondary forests, Dark green x and solid line: Mature forests, Pink ● and solid line: Deciduous forests.

Table 2.4 Permutation test results for axes in RDA

	Df	Var	F	N.Perm	Pr(>F)	
RDA1	1	1.13493	167.8644	199	0.005	**
RDA2	1	0.24052	35.5746	199	0.005	**
RDA3	1	0.02895	4.2826	199	0.015	*
Residual	236	1.5956				

Table 2.5 Permutation test results for the explanatory variables in the RDA

	Df	Var	F	N.Perm	Pr(>F)	
Canopy	1	0.40493	58.1151	99	0.01	**
Coniferous	1	0.317	45.4955	99	0.01	**
USSpRich	1	0.41415	59.4392	99	0.01	**
TreeNb	1	0.04626	6.639	99	0.01	**
MeanDBH	1	0.04509	6.4719	99	0.01	**
ShanDBH	1	0.01819	2.6105	99	0.07	.
SCIh	1	0.0538	7.7215	99	0.02	*
USCover	1	0.0194	2.784	99	0.05	*
Luminance	1	0.08227	11.8074	99	0.01	**
Simpson	1	0.00332	0.4761	99	0.60	
Residual	229	1.5956				

The association of high luminance and canopy closeness in deciduous forests (DF) can also be related to the high scores of saturation complexity in these plots. Light penetrates through the canopy with many variations in light quality depending on the superposition of leaves. The projection of the light onto a relatively homogeneous surface like bare ground or a continuous cover of dead leaves could create complex patterns of Saturation associated with low Hue complexity. Hence, the interaction between complex light pattern and the absence of an understorey could lead to this specific characteristic of patterns in deciduous forests.

Also, instead of bringing complexity to vertical patterns by creating original associations between objects as was expected, the heterogeneity of vegetation layers ('SCIh') actually contributes to bring order to images, hence decreasing their complexity. Thus plots with the highest heterogeneity of layers like MF and SF are also overall the plots with the most regular patterns. The relationship between

complexity and species diversity in the understorey ('USSpRich') is also negative: instead of leading to original arrangements in pixel patterns as was expected, species diversity contributes to the regularity of forests scenes especially for Saturation patterns.

The differences that appear between closed mixed-wood forests (MF and SF) and partial cuts (PC35%, PC50%) are mainly caused by their values of complexity for Hue and Brightness patterns which are higher for most partial cuts and seem to be related to their high luminance and hence to more open canopies and also to a low density of trees ('TreeNb') and low DBH diversity ('ShanDBH'). In harvested plots (PC35%, PC50%), the removal of trees obviously contributes to open the canopy, decrease the density and the average diameter of trees and the diversity of their sizes. As a consequence, more elements of the understorey and soil appear in-between trees: the soil is often visible in canopy gaps and can be associated with leaves or trunks in the pictures, bits of sky may also appear associated with trees trunks therefore producing complex patterns created by original associations between forest objects.

Disturbances hence seem to have a positive effect on the complexity of forest patterns when their impacts are sufficiently strong to obliterate a complete layer from the vertical vegetation; as for example in partial cuts when the canopy is completely open, or in deciduous forests where the understorey is completely absent.

2.5 Discussion

2.5.1 Relationship between the complexity of forest stratification and the structure of tree populations

We found that the heterogeneity and diversity of forest plots are negatively related to the complexity of patterns as described by MIG indices. This result contradicts our first hypothesis of a direct positive link between heterogeneity, diversity and complexity. However, the corollary to that and our second hypothesis is

still confirmed as high percentages of coniferous trees and high tree density are also both negatively correlated to complexity indices.

Mixed-wood closed-forests (SF and MF) both have high tree density and heterogeneous vegetation layering which mean that more vegetation layers are intercepting the understorey light. The canopies of closed forests are also denser with fewer gaps resulting in a more homogeneous penetration of light within the stands and thus in lower complexity of Brightness patterns. The low complexity of Hue and Saturation patterns in both secondary and mature forests could also be directly affected by that gradient of light as colours tend to fade in darker scenes which results in more homogeneous patterns. Another explanation for the lower values of complexity of Hue and Saturation patterns is that a dense layering of tree branches and dense understorey tend to fill the photos with uniformly green vegetation and thus produces regular patterns.

However, it is also possible that our choice of index to represent the layering of vegetation ('SCIh') is too integrative as it represents both the spatial distribution and diversity of heights (Zenner, 2000). The SCI actually has a strong positive relationship with tree density (Zenner and Hibbs, 2000). As a consequence, dense and vertically heterogeneous populations have very high SCI scores, but fill the available canopy space with vegetation and thus appear regular in pictures. The use of a set of indices describing the density, vertical distribution and horizontal heterogeneity of vegetation layers separately instead of one integrated index may allow a better understanding of the effects of vegetation layers and of the interactions between the diversity of layers and their spatial distribution on complexity. However, such indices are often based on visual estimations of the density and distribution of vegetation layers and are therefore strongly based on the subjectivity or experience of the evaluators (McElhinny *et al.*, 2005). Alternatives to visual estimations are based on the interpolation of point sampling for each individual layer and can be very time consuming in the field unless remote sensing tools such as LIDAR are used

(Jaskierniak *et al.*, 2011 ; Wilson, 2011). Considering the potential of digital photos to increase the resolution of sampling and their rapidity of execution in the field, a new method could probably be derived to quantify the density and distribution of layers of vegetation in the photographs (Marsden *et al.*, 2002).

2.5.2 Effects of disturbances on structure and complexity

Using the opening of the canopy as an indicator of tree harvest and the absence of understorey as an indication of heavy browsing, it appears that the effects of both types of disturbances contribute to increase the complexity of forest measured by the MIG for Hue, Saturation and Brightness patterns by comparison with closed undisturbed forests (MF and DF). We showed that disturbances which only partially remove the biomass of the forests can increase the complexity of forest patterns. However, since we did not sample heavily disturbed forests (e.g. clear-cuts or plantations), the effects of high intensities of disturbances on the complexity could not be directly observed. Nevertheless, it can be logically argued that a complete removal of all forest layers (clear-cuts) or the standardisation of forest objects (plantations) should lead to a homogenisation of patterns and a reduction in MIG complexity.

In contrast, the indices of species diversity and heterogeneity are actually higher for undisturbed plots (UScover, USSpRich) or showed no differences related to the degree of disturbance (ShanDBH, SCIh).

Also, interestingly, both MIG and the various indices of diversity or heterogeneity reflect a large variability of possible responses to partial-cuts (see distribution of PC35% and PC50% plots in both PCA in Figure 2.6 and Figure 2.7). Such an increase in the variability of species composition has already been observed in managed forests, but this variability did not translate into changes in the structure of forests (Crow *et al.*, 2002). Harvest operations are generally associated with a diversification of species caused by an increase of ruderal and open-area species, but

also with a simplification of the structure promoting even-aged stands and a decrease of understorey biomass (Torras and Saura, 2008). In our particular case, the large variations in the complexity values for both of the PC forests studied are probably related to the design of partial-cuts: as the cuts are strips (see Figure 2.1), the cuts do not affect all subplots in the same manner. In the PC35% some subplots probably remain unaffected and more resemble uncut forests than disturbed plots. On the other extreme, subplots located in the harvest tracks are disturbed and their structure and complexity reflects the disturbances. On the other hand, with narrower retention bands, all of the PC50% subplots are affected by disturbances and are clearly differentiated from closed-forests (SF, MF, DF). The design of the partial-cuts therefore bares a significant influence over the resulting heterogeneity of forest plots. Variable harvest intensities in forest plots directly influences the structure of the forest and the distribution of trees depending on the location of the subplots, but as shown in previous work on modelled forests (Beaudet *et al.*, 2011) the design of partial-cuts (gaps, different distributions of bands) also causes strong variations in the profiles of light distribution in the understorey. The effects of partial-cut designs on both the structure of forests and the penetration of light is naturally translated in MIG results as they integrate patterns of forest objects, of light and the interactions between light and objects.

2.5.3 Visual obstruction, perspective and light: Unexpected patterns

It appears that the importance of light, perspectives in photos and the interplay between foreground and background are either predominant limitations to the MIG method or that they illustrate the emergence of patterns beyond the simple inventory of structural elements and objects.

The most complex patterns emerge from systems with a dense and diverse understorey and structures emerging from cuts (canopy gaps, DBH evenness and low tree density) or on the contrary in forests with no understorey and some heterogeneity in the penetration of light through a closed canopy. In both cases the complexity of

patterns in the photos emerges from the apparent juxtaposition in the photographs of elements that are spatially separated. In contrast, forests that appear regular are generally heterogeneous, with high species diversity and layering, but the density of the foreground layers masks the heterogeneity of the other objects. The regular patterns in photos from closed forests are therefore composed of objects that are also close to each other in the forest. Hence, considering the emergence of complex patterns, the vertical heterogeneity of the different layers might be less important than the interaction with the density of layers or less important than the horizontal heterogeneity of layers (distribution of gaps within each layer of vegetation).

Complex patterns also emerge from the interactions between light and forest objects. Complex patterns of Brightness appear to be the result of variations in the reflection or the absorption of light on the surface of forest objects and patterns of Saturation in deciduous forests emerge from the interplay between leaves permeability and the absence of understorey. These patterns of light could be integrated to the study of light intensity and availability (Canham, 1988 ; Bellow and Nair, 2003 ; Beaudet, Messier and Leduc, 2004) in forests as the patterns of light quality can be interpreted as a representation of the diversity of light-related niches for regeneration.

2.5.4 Why use MIG for the understanding of forest functioning and management?

The approach that we used to measure complexity in this research is original for several reasons. MIG is part of a new generation of descriptors of forest structure that is based on the representation of patterns rather than on the inventory of definite objects. Patterns can be identified by their shapes and spatial similarities (forest patches (Moser *et al.*, 2002), gaps (Vepakomma, St-Onge and Kneeshaw, 2011)...) or by a statistical criteria or ecological signalling (e.g.: the quality of light under forests (Endler, 1993), variations in biodiversity through time or space (Wiegand *et al.*, 2007), and contour maps of the canopy (Zenner and Hibbs, 2000)). Earlier methods, that are still in use today, for the study of patterns in photographs are generally based

on the recognition of objects (branches, canopy gaps, edges...) (Marsden *et al.*, 2002 ; Kashian *et al.*, 2004) and very few are applied to the emerging patterns and statistical properties of the image. The alternate definition of forest patterns that we propose implies the need for a different set of tools for their description. MIG may thus bring a new perspective on patterns for the study of forests, as it allows capture of the patterns that emerge from the interactions between individual objects and between forest objects and light conditions. Moreover, an index such as the MIG based on quick and repeatable sampling (photographs) has a good potential to be integrated to a large array of forest studies as it can be applied in photos from within the forest as we did, but also on aerial photos or pictures from more specific compartments like soils, understorey plant communities or canopy distributions. The use of photographs could also permit long-time surveys of the variations of complexity of patterns in different seasons or years. Links between these time series and different processes could then be made. For example, studies considering light availability and regeneration niches (Beaudet and Messier, 2002 ; Beaudet, Messier and Leduc, 2004) could profit from such indices of complexity that would bring a spatial dimension to light intensities measures. MIG could also bring an additional metric for habitat description for several areas of research considering the perception of the habitat by animals. Notably the complexity of patterns is linked to visual obstruction of vegetation and to effects of perspective; these two features of forest scenes could be related to the behaviours and movements of animals in forest systems, notably considering their response to forest edges (St-Laurent *et al.*, 2008). Moreover, different researchers have shown the importance of the patterns of colours and light in the habitat for food foraging, intra-specific interactions, habitat selection and escape patterns (Endler, 1993 ; Fleishman *et al.*, 1997 ; Schaefer and Kappeler, 2010). The complexity of these patterns could be examined directly using MIG to observe if the complexity of colour associations influences the recognition of food or shelter by fauna.

Finally, different research on the perception of forests and other ecological systems by humans showed that the visual representation of the scenes were often more important to form an opinion about their management than the rational analysis of their composition (Karjalainen and Tyrvainen, 2002 ; Kim, Lee and Shelby, 2003). Notably, the recognition of complex patterns like fractals in natural scenes has been acknowledged as a good indicator for the acceptability of landscapes (Hagerhall, Purcell and Taylor, 2004 ; Hunt and Haider, 2004 ; Dramstad *et al.*, 2006). The use of MIG as a rational tool to measure the complexity of the pictures presented for acceptability surveys could lead to a better understanding of the motivations behind choices based on visual discrimination.

2.6 Conclusions

We showed that heterogeneity and biodiversity of closed-forests tend to create regular patterns within forest communities as the forest scenes are filled with vegetation. On the other hand, forests that were partially-cut are more complex as they allow original patterns to occur from the interactions between objects located in different forest layers (canopy, understorey, soil, trees...) therefore suggesting that some moderate disturbances might allow an increase in complexity and thus promote a reorganisation of forest objects. The patterns created by light in forest communities also proved especially important in the differentiation of forest types.

The interactions between forest objects and light patterns are probably the most interesting new determinant of complexity in patterns identified thanks to the MIG method. These patterns could bring more information regarding the understanding of the relationship between habitat patterns and the use of space and resources by various organisms and also regarding the social acceptability of management practices.

2.7 Appendices

Table of appendices for Chapter 2

Appendix 2.1 Method for the testing of autocorrelation between MIG values in the photographs

We tested the spatial autocorrelation of the MIG values calculated from the photographs using Geary's index of spatial autocorrelation.

The photographs are all distributed in the plots every 10 meters on straight lines parallel or perpendicular to the axis of the plot (see map of photo sample points in Figure 2.2). Neighbours are thus defined as two contiguous photographs that are taken in the same direction (parallel or perpendicular to the axis of the plot). Additionally, the neighbouring indices are directional, and defined according to the direction in which the photographs were taken. Basically, photograph B was considered a neighbour to photograph A if the two photographs were located on the same line, hence pointing in the same direction, and photo B was in front of photo A. In this example, photo B is a neighbour to photo A, but photo A is not considered a neighbour to photo B.

The results of the autocorrelation test are presented as a table in Appendix 2.2. The table only contains the autocorrelation values for the plots with significantly autocorrelated MIG values (p-values < 0.05). Negative Geary indices indicate that the values are more different than expected with no spatial autocorrelation, whereas positive values indicate that the values are closer than expected with no spatial autocorrelation.

Appendix 2.2 Autocorrelation table for MIG values

	Canopy Hue	Canopy Saturation	Canopy Brightness	Mi-forest Hue	Mi-forest Saturation	Mi-forest Brightness	Understorey Hue	Understorey Saturation	Understorey Brightness
PC50% 1	0	0.47	0	0	0	0.33	0	0.44	0.48	0.43
PC50% 2	0	0	0	0	0	0	0	0	0	0
PC50% 3	0	0	0	0	0	0	0.43	0	0	0
PC35% 1	0	0	0	0	0	0	0	0	0	0
PC35% 2	0	0	0	0.72	0	0	0	0.39	0	0
PC35% 3	0	0	0	0.45	0.28	0	0	0	0.34	0.31
SF 1	0	0	0	0	0	0	0	0	0	0
SF 2	0	0	0	0	0	0	-0.54	0	0	0
SF 3	0	0	0	0	0	0	0.29	0	0	0
MF 1	0	0	0	0	0.39	-0.47	0	0	0	0
MF 2	0.31	0.34	0	0	0	0	0.31	0	0	0
MF 3	0	0	0	0	0	0	0	0	0	0
DF 1	0	0	0	0	0	0	0	0	0.32	0
DF 2	0.38	0	0	0	0	0	0	0.45	0	0
DF 3	0	0.37	0	0.61	0	0	0	0	0	0

CHAPITRE III

DO PARTIAL-CUTS CREATE FOREST COMPLEXITY? A NEW APPROACH TO MEASURING THE COMPLEXITY OF FOREST PATTERNS USING PHOTOGRAPHS AND THE MEAN INFORMATION GAIN

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3.1 Abstract

Structural complexity is increasingly cited as an objective of sustainable forest management. Such complexity at the stand level is normally associated with an uneven or heterogeneous distribution of herbs, shrubs and live and dead trees. In forest ecosystems, management aimed at promoting complexity would therefore imply increasing heterogeneity in the tree layer, to promote the emergence of multiple layers of vegetation and to encourage the restoration of natural structures and processes. Following the hypothesis that intermediate disturbances are necessary to increase the biodiversity of forest communities, initiatives have been proposed to use partial cuts to increase the heterogeneity and complexity of forests. Both the applicability of the intermediate disturbance hypothesis and the effects of partial cuts on complexity need however to be tested. Yet, indices capable of measuring the complexity of forests are still rare and often require long time series or high resolution data. We introduce a novel and direct measure of the complexity of emerging patterns in forest stands using an index of the mean information gain (MIG) calculated using digital photographs. With this method, the effects of two different intensities of partial cuts on the complexity of forest patterns were compared to the values found in closed-forests in mature and secondary mixed-wood boreal stands. The relationship between canopy opening, as an indicator of disturbance, and the complexity of forest patterns was confirmed showing evidence of an 'intermediate disturbance effect' for the complexity of patterns.

Our results show that partial cuts increase the overall complexity of forest patterns as compared to uncut closed-forests. We also found evidence that the intermediate disturbance hypothesis can be applied to the complexity of forest patterns as measured by the mean information gain method used in this study.

Keywords: Complexity, Heterogeneity, Light, Digital photographs, Partial cuts, Ecosystem management, Intermediate disturbance hypothesis.

3.2 Introduction

Concerns for the maintenance of biodiversity and resilience of forest systems and the impact of various forestry practices in maintaining these two elements have increased in recent decades. The impact of forest fragmentation at the landscape level and forest simplification at the stand level on species reductions and disappearances have raised concerns and pushed policy-makers and forest managers to adopt new practices aimed at maintaining or favouring the natural complexity of the forest. Managing for complexity (Puettmann, Coates and Messier, 2009) has therefore recently emerged as a new objective in forest management. The integration of complexity into forest management would involve designing harvest operations that maintain or enhance the capacity of the systems to evolve and adapt to changing conditions. Operationally, managing for complexity involves conserving or recreating complex patterns in the distribution of forests structures and objects (Heinimann, 2010). This complexity of patterns and the various associations and spatial configurations between objects should guarantee the conservation of processes (Turner, 1989).

Partial cutting has been proposed as a method of increasing the proportion of uneven-aged and structurally heterogeneous stands. This approach is based on the theory that by creating gaps in closed even-aged forests or by leaving structural legacies in harvested plots, the structural complexity of the systems will be enhanced earlier in the regeneration process, and thus the functions and spatial patterns associated with older more complex forests will be restored faster and more efficiently (Drever *et al.*, 2006). Disturbances can be considered to be part of the cycle of resilience of forests as they allow for a reorganisation of the system and thus for an adaptation to new environmental conditions (Holling, 2004). In the case of closed even-aged forests, harvesting can be used as an opportunity to increase the adaptive capacity of forest systems (Gunderson, 2000). If the complexity of forest

patterns is an indicator of forest organisation and adaptability (i.e. it reflects the diversity of associations and processes), then, partial-cuts could be used to induce an increase of resilience by increasing the complexity of spatial patterns.

Moreover, the intermediate disturbance hypothesis (IDH) (Connell, 1978 ; Denslow, 1985) proposes that species diversity should be highest when moderate disturbances occur in an ecosystem. Moderate disturbances should not only allow the coexistence of species associated with severe disturbances and of species associated with light infrequent disturbances, but should also limit the abundance of dominant competitive species and thus allow an increase in the proportion of less common species (Connell, 1978 ; Denslow, 1985). As a potential for reorganisation and for the introduction of new species and new structures, we extend the concept and propose that intermediate disturbances could have a positive effect on the complexity of forest patterns by diversifying the possible spatial associations between forest objects (Proulx and Parrott, 2008).

Operational integrative indices of complexity that can be used to verify the effect of forest management on forest complexity and thus the applicability of the intermediate disturbance hypothesis are however still rare in forest ecology. Few previous studies have actually investigated the effects of new harvest strategies on the complexity of forest patterns. Instead, earlier studies have looked at the relationship between species and structural diversity. Years of study have thus led to knowledge on the response of specific structures such as living trees (Crow *et al.*, 2002 ; Brais *et al.*, 2004 ; Saunders and Wagner, 2008), dead wood, (McGee, Leopold and Nyland, 1999) and understorey plants (Roberts, 2007) to different types of harvesting. On the other hand, the effects of partial-cuts on the spatial distribution of structure and habitat heterogeneity have also been studied for different animal taxa (Suzuki and Hayes, 2003 ; Loehle *et al.*, 2005 ; Aguilar-Amuchastegui and Henebry, 2007). Considering this early work, the complexity of forests can be defined as the product of species and structural diversity and spatial heterogeneity. As a consequence, much

research has attempted to measure the complexity of forests at different scales as a combination of indices of both diversity and heterogeneity (Van Den Meersschaut and Vandekerkhove, 1998 ; Staudhammer and LeMay, 2001). These indices are generally very thorough in their description of the structural composition of forest plots, accounting for several compartments (dead trees, lie trees, understorey structure, canopy...) and for the variability of that composition (Van Den Meersschaut and Vandekerkhove, 1998), but are actually often lacking a description of the spatial structure of the system. Hence most structural indices give a complete idea of the diversity of the composition of forest for a given plot size, but lack a description of the spatial associations between objects. Several attempts have however been made to capture the spatial components of forest structures, and to represent the association of the different objects (Barbosa Lima *et al.*, 2006 ; Pommerening, 2006 ; Wiegand *et al.*, 2006 ; Grabarnik and Särkkä, 2009 ; Kretzschmar, Soubeyrand and Desassis, 2010) with interesting outcomes regarding the importance of pattern characterisation for the understanding of forest processes. However, since the dominant approach to spatial patterns in ecology has until recently been point pattern analysis, the amount of data (and consequent noise) required to achieve a quantitative and understandable response tends to be overwhelming.

A relevant measure of complexity in forest stands should therefore include descriptors of both diversity and spatial distribution and some account of the interactions between them, while at the same time remaining operationally measurable.

Again, different attempts have been made to develop such an index and especially using emergent patterns. Emergent patterns are actually the visible results of the spatial associations between forest objects (trees forming forest patches in a landscape, forest edges defined by individuals, canopy gaps delineated by the foliage...) and can be studied as objects, by defining their shapes (regularity, fractal dimensions...) (Sugihara and M. May, 1990 ; Hagerhall, Purcell and Taylor, 2004),

dimensions (surface area, perimeter, richness of components...) and spatial characteristics (aggregation, spatial autocorrelation) (Zenner and Hibbs, 2000 ; Marsden *et al.*, 2002). The characterisation of emergent patterns as complexity indicators is compatible with the use of remote sensing methods such as digital photographs }(Marsden *et al.*, 2002), aerial photograph (Hagerhall, Purcell and Taylor, 2004) or LIDAR (Vepakomma, St-Onge and Kneeshaw, 2008 ; Kane *et al.*, 2011).

The method we use in this paper is actually a new approach to the characterisation of patterns in digital photographs based directly on the distribution of pixels. Rather than defining shapes from the delineation of objects, the pixels are used as individuals and the interactions between the composition of the pattern (the colours of pixels) and the spatial distribution of individuals is measured directly.

We expect that intense disturbances, such as clear-cuts, that tend to leave only bare soils and open skies, will have very regular spatial patterns on photographs. On the other hand closed forests should also appear relatively regular as they are formed of multiple layers of vegetation creating a uniform green pattern. We expect that intermediate disturbances that allow interfaces to appear between closed forests and open areas would increase the complexity of the resulting patterns. An index based on the complexity of spatial associations in photographs should thus capture the variation in the structure of the forest stand.

In this paper, we specifically test this approach to measuring complexity by comparing the complexity of forest patterns emerging from different management histories (former clear-cuts, maturing forests, partial-cuts). Our purpose with these comparisons is to (1) verify whether our index is able to capture an increase in the complexity of forest patterns caused by partial harvesting in closed forests, and (2) to evaluate whether the intermediate disturbance hypothesis is applicable to the complexity of patterns in forests.

3.3 Methods

3.3.1 Study area

All study sites were located in the ecosystem management area of the TRIAD project near the town of La Tuque (47° 26′ 00″ N, 72° 47′ 00″ W) in central Quebec, Canada. The TRIAD project is based on using three different management objectives (conservation, ecosystem management and intensive management) within the 0.86 million hectares forest management unit. The different land-uses are spatially distributed in order to optimize the associations between these different land-uses at different scales (Tittler, Messier and Burton, 2001 ; Messier *et al.*, 2009). Each component of the TRIAD zone has different but complementary objectives: 1) the conservation zone aims at allowing forest aging and colonisation by late succession species, 2) the intensive forestry zone is based on the plantation of fast-growing species and aims at partially compensating the loss of wood production caused by the conservation area, 3) the ecosystem management zone involves different intensities of harvest methods ranging from traditional clear-cuts to partial cutting. The partial-cuts in the ecosystem management zones of the TRIAD project were designed with the objective of increasing the proportion of uneven-aged and heterogeneous stands.

3.3.2 Sampling

All study sites were included within a 2.5 km radius area at the northern limit of the mixed-wood conifer and hardwood forest in Haute-Mauricie (Qc) Canada. The study forests are dominated by balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), red maple (*Acer rubrum*) and yellow birch (*Betula alleghaniensis*). The sampled forest stands originated following a major fire in 1923. We sampled four different forest treatments corresponding to different forest histories .All forest treatments originated from a major fire in 1923 and were then managed differently. Mature forests (MF) were left untouched, secondary forests (SF) were clear-cut during the 1970's and are untouched since. Partial-cut treatments (PC50 and PC35)

were both partially harvested during the winter of 2007-08 (see Table 3.1 for an overview of the history of the forest treatments).

Table 3.1 History of the forest treatments

MF	SF	PC35%	PC50%
1923 Fire			
Some low level selective cuts	1970's Clear-cuts		
		2007 partial-cut (35% basal area)	2007 partial-cut (50% basal area)

Both partially cut forests were harvested with the same basic technique. A 5 m wide temporary track was clear-cut, and from that track two 7 m wide strips are thinned to ~50% of their basal areas. Between these harvested strips retentions areas of respectively 5 m and 19 m for PC50 and PC35 were left uncut in order to attain a total 50% or 35% basal area removal (see Figure 3.1 for an illustration and explanation of the harvest design).

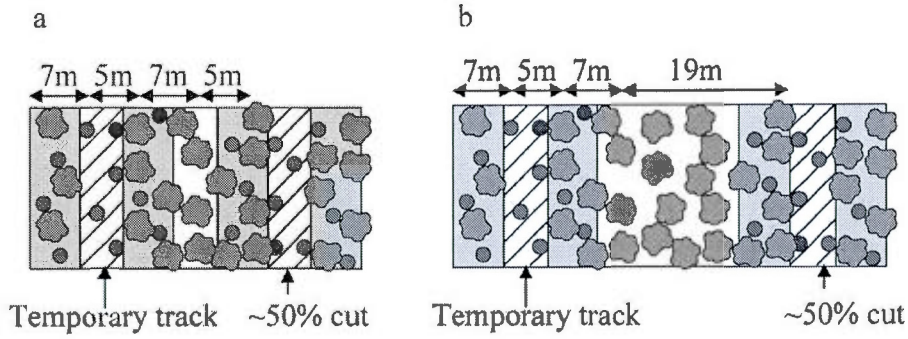

Figure 3.1 Harvest designs for (a) 50% partial-cut (PC50%) and (b) 35% partial-cut (PC35%). The partial-cuts are organized around 5 metre wide skid trails (white) that are clear-cut. About 50% of the basal area is harvested from two 7 metres wide bands (grey bands) on each side of the skid trails. These cut blocks are separated by uncut bands (white bands) of varying width: 5 metres in PC50% (a) and 19 metres in PC35% (b).

In each treatment we inventoried and photographed three 40x40 m repetition plots during the summer of 2008 (PC35 and PC50) and 2009 (MF and SF).

3.3.3 Photographs sampling

Sixteen 10x10 m sub-plots were photographed in each of the twelve (4 treatments x 3 repetitions) 40x40 m plots (Figure 3.2.a). As two of the forest treatments involve partially cut strips, and in order to avoid the directional effects of the vegetation structure that resulted from that harvesting design, each subplot was photographed in two perpendicular directions (see Figure 3.2.b).

Photographs were taken at each of the photo-points from three different angles, with the camera pointing to 3 different layers of the forest structure (see Figure 3.2.c and Table 3.2 for the camera settings). Canopy photographs were taken with a +45° inclination of the camera; mid-forest layer photographs with a 0° inclination and finally the understorey photographs with a -30° camera inclination (see Figure 3.3 for examples of the resulting photographs).

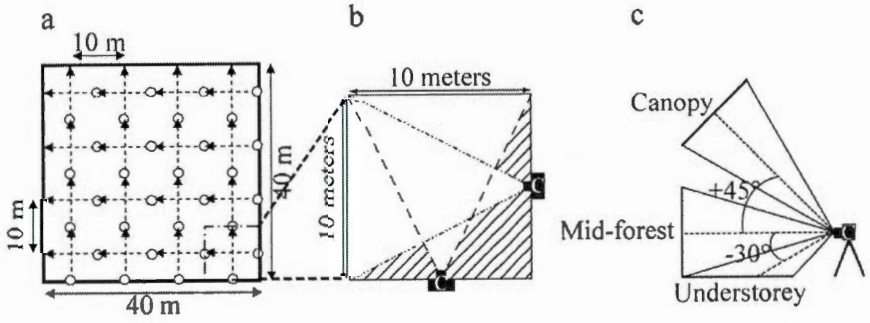

Figure 3.2 a: Schematic map of a 40x40 m plots with the different positions of the camera (open circles) and the directions of the photographs (dashed arrows). b: Schematic representation of photographic sampling in 10x10 m subplots. Hatching represents the dead angles of the cameras. c: Angles of the camera for the three layers of vegetation (canopy, mid-forest, understorey). Dashed lines represent the centre of the photographs with the angles of inclination for the camera.

This design results in 16 pairs of photographs for each of the twelve 40x40 m repetition plot and each layer of vegetation (Canopy, Mid-forest and Understorey), each corresponding to a 10x10 m subplot.

Figure 3.3 Examples of photographs from the 3 forest layers. Canopy (a & d), Mid-forest (b & e), Understorey(c & f), in maturing forests (MF, a, b & c) and 50% partial-cut (PC50%, d, e & f).

Table 3.2 Camera settings (see Proulx and Parrott, 2008 for more explanation about the choices behind these settings)

Setting	
Camera	Canon EOS Rebel XTI 400D
Focal length	18 mm
Aperture diameter	6.3 mm
Focus distance	10 m
Tripod's head above ground	1.3 m
Depth of field (DF)	2 m - infinity
Exposure mode	Aperture priority
Time window for shooting	7h00-16h00
Visual obstruction < DF	Avoided
White balance mode	Natural light
Resolution	1288 x 1936 pixels

3.3.4 Measuring complexity: the Mean Information Gain (MIG)

The description of the complexity of vertical patterns in forests is generally summarized by variations in canopy heights (Zenner and Hibbs, 2000) or by visual estimates of the variations in the density of vegetation layers (Neumann and Starlinger, 2001 ; McElhinny *et al.*, 2005). These methods are perfectly valid for the estimation of the diversity of structures but do not contain enough detail and are not precise enough to be applied to the measure of patterns complexity. As a consequence and in order to develop an integrative measure of complexity for forest communities, we chose to implement a method based on the measure of the Mean Information Gain (MIG) in photographs, developed by Proulx and Parrot (2008). The method consists in measuring the complexity of patterns in digital photographs of the vertical structure. Digital photographs provide and intensive sampling of all the visible objects that constitute the vertical structure of the forest stands. The values of each pixel represent the colour characteristics and hence the observable differences between the objects that were photographed. The spatial associations of pixels in the resulting 2D pictures reproduce the visible patterns of the spatial distribution of these objects. The complexity of the patterns can therefore be measured directly on the matrices of pixel values in the photos. This sampling method also provides a

repeatable and potentially automatable method to monitor the complexity of forest systems over large surface areas or in time.

The MIG is a measure of the complexity of patterns based on Kolmogorov information complexity (Li and Vitányi, 1994). In simple words, the MIG allows us to measure the disorder of a pattern by quantifying the length of its description. A regular pattern like a checkerboard (see Figure 3.4.a) for example, is identified as a simple ordered pattern as its description only requires the dimensions of the pattern (8x8 pixels) and the identity and sequence of the pixels (White-black). On the other hand, in order to describe a completely random pattern with the same level of precision, each individual pixel must be described as their identity or position cannot be predicted from their neighbours. Random patterns are therefore described as maximally disordered. MIG values range between 0 and 1, regular patterns are characterised by low values and random patterns by high values. As complex ecological patterns are considered to be neither completely regular nor completely random (see Figure 3.4.b), the most complex patterns are represented by intermediate values of MIG (Andrienko, Brilliantov and Kurths, 2000 ; Parrott, 2005 ; Dale, Anand and Desrochers, 2007).

3.3.5 MIG computing

Digital images can be encoded in different colour formats. Traditionally digital cameras record the pictures in RGB (Red Green Blue) format, but for a more direct link to the actual colour of objects and effects of light, our photographs were converted to HSB images (Hue Saturation Brightness) following the method proposed by Smith (1978). Each pixel in the image thus bears 3 values respectively defining its colour (hue), the intensity of the colour (saturation) and the quantity of light it received (brightness).

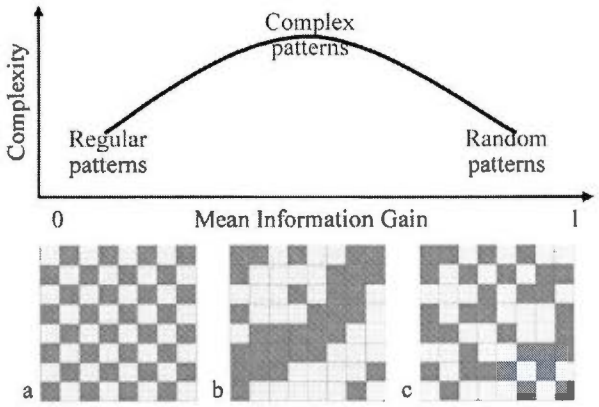

Figure 3.4 Convex relationship between Mean Information Gain (a measure of complexity based on the length of the description of the pattern) and the complexity of spatial patterns. a) Regular pattern, b) complex pattern, c) random pattern. Note that although the three patterns (a, b and c) have the same pixel composition (white and grey pixels) their MIG increases as an effect of the increasing spatial association between white and grey pixels.

The values of pixels in the HSB domain are originally continuous numerical values, but were clustered into a smaller number of classes of values for the computing of MIG. This clustering of values is necessary as with continuous values, each pixel can potentially be unique, and can thus result in false random patterns. The final number of classes of values (N) is limited by the resolution of the images and by the size of the associations of pixels (n) considered in the computing of MIG. The ratio of the resolution to the maximum number of possible combinations between n pixels must remain superior to 100 in order to exclude the possibility of false-random patterns (see Eq. 1).

$$\frac{\text{Resolution}}{N^{n}} > 100 \qquad \text{Eq. 1}$$

In our case, for pictures of resolution =1288x1936 pixels and n =2x2 pixels, we chose to reduce the number of classes for each band to N = 10 classes (for a ratio ~250).

Once the image is converted to HSB and the number of classes of values is reduced, the 3 data matrices of hue, saturation and brightness values can be used to calculate the complexity of the patterns of pixels. The MIG is computed directly on the diversity of the spatial associations of 2x2 pixels for each band (HSB) of the photographs using Eq. 2 (Andrienko, Brilliantov and Kurths, 2000 ; Proulx and Parrott, 2008):

$$MIG = \frac{H[\chi] - H[\gamma]}{\log N^4 - \log N^1} \qquad \text{Eq. 2}$$

N^4 is the maximum number of 2x2 combinations of pixel values, $H[\chi]$ is the Shannon diversity of 2x2 pixels associations (see Eq. 3), and $H[\gamma]$ is the Shannon diversity of individual pixel values in the image (Eq. 4) (see also Figure 3.5 for an illustration of patterns and their associated values of diversity for pixel associations and individuals).

$$H[\chi] = -\sum_{i=1}^{N^4} p(\chi\iota) \log p(\chi i) \qquad \text{Eq. 3}$$

$p(\chi i)$ is the probability of finding a specific 2x2 combination χi of pixel values in the image

$$H[\gamma] = -\sum_{i=1}^{N} p(\gamma\iota) \log p(\gamma i) \qquad \text{Eq. 4}$$

$p(\gamma i)$ is the probability of observing a pixel value γi independently of its location in the image.

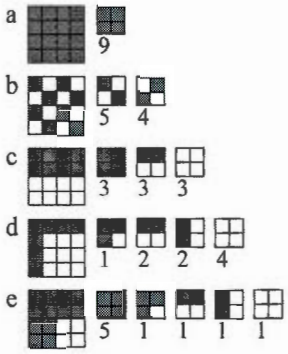

Figure 3.5 Examples of patterns created with N=2 classes of pixels values (black or white) with increasing complexities (MIG values: a=0, b=0, c=0.19, d=0.28, e=0.35) and the list of 2x2 pixel associations that compose them, the number below each pixel association is its number of occurrence in the pattern. The resulting diversities of spatial associations H[χ] are: a=0, b=0.69, c=1.10, d=1.27, e=1.30 and the diversities of individual pixel values H[γ]:a=0, b=0.69, c=0.69, d=0.69, e=0.56.

MIG indices are computed for each photograph independently and then the MIG values are averaged within the pairs of photographs corresponding to each 10x10 m subplot. This results in 48 values of MIG for each combination of layer (Canopy, Mid-forest and Understorey) and HSB band in each forest treatment.

All computing for MIG measures of the digital photos was done using MATLAB (V 7.6, 2008).

The values of MIG in the hue band show the complexity of spatial associations between the colours in the photographs and are therefore related to the potential for spatial associations between objects of different nature (white sky and green leaves, leaves or trunks of different shades, green vegetation and brownish bare soil...). The interpretation of Saturation patterns is based on the interactions between the light and the colour of forest objects. Hence, low values of Saturation can be achieved either because the colour of the objects is actually dull, or because the object is in plain light or in the shade as both bright and insufficient light tend to fade the colour of objects. In the case of forests, the scenes are generally dark, and the apparent saturation of

colours increases with brightness. The patterns in the brightness band represent the complexity in the distribution of light and its interactions (reflection, absorption) with the objects in the photographs (trunks, leaves, soil...). As patterns in the saturation and brightness bands are closely correlated and as the patterns of brightness are more directly related to ecologically relevant characteristics of forest objects, we chose to only present the results for the complexity of patterns in the hue and brightness bands.

Each treatment is thus represented by 48 MIG values for each of the 6 combinations between 2 bands (hue and brightness) and 3 vegetation layers (canopy, mid-forest and understorey).

3.3.6 Canopy closure

The 2 photographs of the canopy layer in each 10x10 m subplot were also used to measure the canopy opening (see Figure 3.2.c). These photographs were manually converted to black and white by selecting a threshold level that allows the distinction between the sky and the vegetation. The closure of the canopy for each image is defined as the percentage of the number of black pixels in the image. The final value of canopy closure for each 10x10 m subplot is the average of the canopy closures measured on the two original photos.

3.3.7 Data analysis

The MIG values from each forest treatment were compared using an analysis of variance (ANOVA) with the 40x40 m repetition plots embedded in forest treatments as fixed factors. Tukey's test was used as a post-hoc test to hierarchically differentiate the treatments (R 2.12.2, package: stats) (R Development Core Team, 2010).

The relationships between canopy closure and the complexity of patterns were computed using mixed-effect models with the 40x40 meter plots included as random factor (R 2.12.2, packages: stats, nlme, AICcmodavg) (R Development Core Team, 2010 ; Mazerolle, 2011 ; Pinheiro *et al.*, 2011). Linear and second degree polynomial models for the relationship between forest closure and complexity were tested for

both data from hue and brightness bands and for all the vegetation layers and compared using ANOVAs to select the best fit. The squared correlation coefficients between the observed data and the models were also computed in order to present an estimate for the fit of the models.

3.4 Results

3.4.1 Range of complexity of patterns in managed boreal mixed-wood forests

The values of MIG in our data set ranges from 0.08 to 0.45, all the patterns considered here thus range from very regular (MIG tends to 0) to complex (MIG tends to 0.5). We will therefore consider our gradients of MIG values directly as gradients of complexity with high MIG values representing complex patterns and low MIG values representing regular patterns.

3.4.2 Effects of forest treatments on the complexity of patterns in the hue band

For the canopy layer, both partial-cut forest treatments (PC50% and PC35%) had significantly higher MIG values than the mature forest (for α=0.01, see Figure 3.6.a and Table 3.3.a). Similarly for both lower level canopy layers (Figure 3.6.b and c, Table 3.3.b and c), MIG values were highest for PC50% and lowest for the closed forests (MF and SF). Mature and secondary forests were found to have consistently similar complexity of patterns for all layers (Figure 3.6.a, b and c, Table 3.3.a, b and c). Also, and although no statistical analysis was done, MIG values were clearly higher for the upper canopy layer compared to the two lower canopy layers. The patterns in the canopy layers are thus apparently more complex than in the mid-forest and understorey.

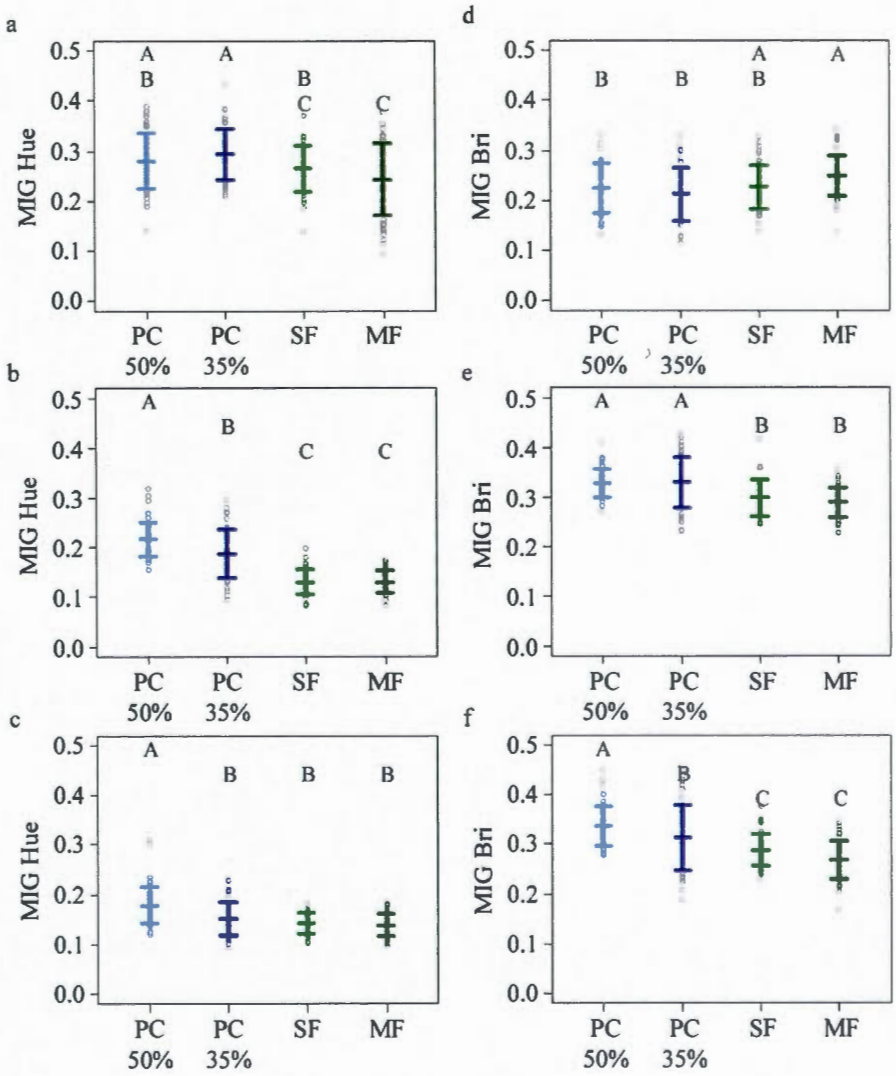

Figure 3.6 Analyses of variance of MIG values for the hue (left) and brightness (right) bands between forest treatments for each of the layers of vegetation (a & d: canopy, b & e: mid-forest layer, c & f: understorey). P-values for anova tests between forest treatments are all <0.01; Intervals represent the standard deviations for each sample; Different letters show significant differences as determined by Tukey post-hoc tests on forest treatments with α=0.05.

Table 3.3 Result tables for the ANOVA between forest treatments and forest plots nested in forest treatments

a) Hue Canopy Photos

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Forest treatment	3	0.067	0.022	9.068	0.000	***
Forest treatment:Plot	8	0.167	0.021	8.436	0.000	***
Residuals	180	0.446	0.002			

b) Hue Mid-forest Photos

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Forest treatment	3	0.264	0.088	90.131	0.000	***
Forest treatment:Plot	8	0.045	0.006	5.734	0.000	***
Residuals	180	0.176	0.001			

c) Hue Understorey Photos

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Forest treatment	3	0.047	0.016	22.022	0.000	***
Forest treatment:Plot	8	0.031	0.004	5.355	0.000	***
Residuals	180	0.129	0.001			

d) Brightness Canopy Photos

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Forest treatment	3	0.035	0.012	5.915	0.001	***
Forest treatment:Plot	8	0.063	0.008	4.030	0.000	***
Residuals	180	0.352	0.002			

e) Brightness Mid-forest Photos

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Forest treatment	3	0.062	0.021	20.399	0.000	***
Forest treatment:Plot	8	0.080	0.010	9.863	0.000	***
Residuals	180	0.183	0.001			

f) Brightness Understorey Photos

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Forest treatment	3	0.129	0.043	30.260	0.000	***
Forest treatment:Plot	8	0.144	0.018	12.652	0.000	***
Residuals	180	0.255	0.001			

3.4.3 Effects of forest treatments on the complexity of patterns in the brightness band

In the canopy layer, the lowest MIG value was found for the PC35% forest treatment and the highest for the mature forest treatment (α=0.01, Figure 3.6.d and Table 3.3.d). However, for both lower layers (mid-forest and understorey), the tendency is to observe decreasing MIG values from the most open stand (PC50%) to the most closed (MF) (Figure 3.6.e and f and Table 3.3.e and f). Contrary to MIG values for hue patterns, brightness patterns tend to be more complex in the lower layers than in the canopy layer.

3.4.4 Canopy closure and the complexity of patterns

The relationships between complexity (as measured by MIG) and canopy closure for the canopy layer are convex for patterns of both hue and brightness (R^2 = 0.27 for hue patterns and R^2 = 0.24 for brightness) (Figure 3.6.a and b). This relationship shows that the complexity of hue and brightness patterns reaches a maximum respectively around 60-70% and 75-85% of canopy closure. This suggests that the complexity of canopy photos is related to the proportion of sky visible through the foliage, with a maximum for slightly open canopies.

In the two lower layers (mid-forest and understorey Figure 3.7.c to f), the relationships between complexity and canopy closure are generally negative with complexity decreasing with increasing canopy closure. Patterns in the hue band appear less complex in closed forests, which support our results among forest treatments. This indicates that the associations of hue values between forest objects are more regular in closed forests and that the same associations of colours are repeated in the image. In the same way, patterns of brightness values are more regular in closed forests with less diversity in the associations of light intensities.

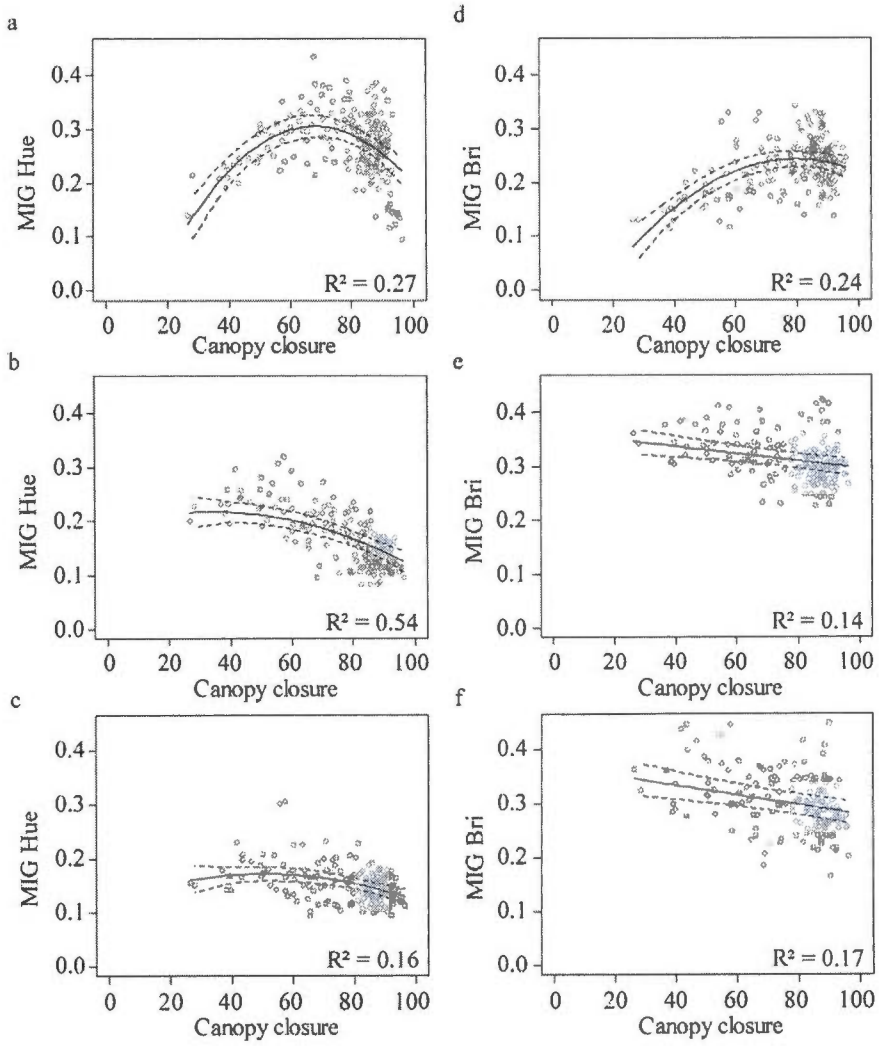

Figure 3.7 Relationships between canopy closure and MIG values (solid lines) for the hue (left) and brightness (right) bands for all forest treatments together for each layer: a & b: canopy, c & d: mid-forest layer, e & f: understorey. Dashed lines represent the 95% confidence interval for the model. The R^2 are the squared correlation coefficients between the observed and the modelled data.

3.5 Discussion

The complexity of patterns as measured by MIG on the digital photos of forests comes from the complexity of assemblages between forest objects and the visual contrasts between these objects. The forest stands identified as complex by the MIG are thus systems that allow a variety of different associations to occur between different forest objects and light intensities (Proulx and Parrott, 2008). Over the relatively small range of forest treatments investigated in this study, partial-cut stands have higher levels of complexity of patterns than closed-forest stands. Also, the relationship between canopy openness and the complexity of patterns indicates that both the highest and lowest intensities of disturbance can induce a decrease in the complexity of patterns (Figure 3.7 a, b, c and e). These findings suggest that partial harvests increase the complexity of patterns in forests and that the effects of these moderate disturbances (i.e. between clear-cut and no harvesting) support the "intermediate disturbance hypothesis" in terms of its application to complexity.

3.5.1 How to interpret the complexity of forest patterns measured in photographs

Understanding the complexity of forest pattern measured by the MIG depends on understanding the relationships between the MIG and more traditional features of forest structure. First, the complexity of patterns measured by MIG is not directly related to species diversity. The diversity of species only affects the complexity of patterns if the species are visually different (in shape, spatial distribution of biomass, colour, reflection or absorption of light...). For example, in our canopy photos, the juxtaposition of two species with foliage of similar shades of green will not increase the complexity of forest pattern in the images. On the other hand the juxtaposition of the sky with leaves (different colours) or different superpositions of leaves (different light intensities) would lead to more original associations between pixels hues or brightness levels and thus more complexity to the patterns. The complexity of patterns measured by MIG may thus be higher in canopies with lower species

diversity but more leaf layering than in very species-diverse canopies but with no layering (see the visual effect of leaf layering in Figure 3.3.a). Also, objects that are visually different but which are clearly separated in the photographs will tend to produce simple patterns when measured with the MIG index as the resulting pattern will be a juxtaposition of uniform areas (for example blue sky over brown soil). Hence, complex patterns emerge from the spatial mixing of different objects and not only from their presence (Witté, Kneeshaw and Messier, In Prep).

The relationship between the complexity of patterns measured by the MIG and light is somewhat more complicated. The MIG measured on the brightness band measures the interaction between light and objects in the forest. Technically, the patterns of light that appear in photographs are only the results of the patterns created by the vegetation. In photographs the light only reveals the position of the objects by being either reflected by their surfaces or obstructed by them. From an ecological point of view however, light and the patterns it creates are determinants for several process from plant regeneration and growth to decomposition and soil chemistry (Endler, 1993 ; Denslow and Guzman, 2000 ; Beaudet, Messier and Leduc, 2004). Thus, the complex patterns in the brightness band that emerge from the irregular distributions of forest objects in space are also representative of the occurrence of various plant and forest processes that are dependent on light distributions.

3.5.2 Partial-cuts allow original associations of forest objects

The removal of some trees in otherwise dense and closed forests by partial-cuts creates new forest patterns (McElhinny *et al.*, 2005). In this study, partial tree harvesting increased the diversity of visible forest objects by mechanically reducing the presence of trees in the photographs. In the mid-forest and understorey layers, the more complex patterns emerging after partial-cuts are therefore caused by original associations between objects from different forest strata (soil juxtaposed with tree trunks, understorey plants associated with the sky due to canopy openings) (Proulx and Parrott, 2008). The increased complexity of hue patterns in the recently partially

cut forests emerged from the reduced density of trees and understorey plants in the pictures (see the example photographs in Figure 3.3). The pictures taken in the partial-cuts thus include patterns with features from both closed forests (uniform green screens of vegetation) and open systems (sky, bare soil and vegetation mixed at all height of the image).

The complexity of patterns in the brightness band is driven by the same type of effects on the structure of forest communities. In the lower layers (mid-forest and understorey) the openness of the canopy allows more light to penetrate through the layers of the community (Beaudet and Messier, 2002) and therefore allows the juxtaposition of very bright areas with darker spots, but also in the same pictures, more subtle gradients of lights in the more densely vegetated areas (see the mid-forest layer in the partial-cuts in Figure 3.3.e). Also, in the case of intermediate disturbances such as partial-cuts, light can reach forest objects from different angles (from the top of the canopy but also laterally through gaps or after being reflected off another surface) therefore increasing the diversity of light intensities on similar objects (Endler, 1993). In undisturbed closed forests, light is strongly filtered through the dense canopy and variations in brightness occur progressively (hence regularly) along the vertical gradient of light.

In the canopy layer, however, partial-cuts create large contiguous canopy openings and therefore a radical increase of incoming light. The intensity of light in that layer tends to increase the contrasts between bright sky and darker objects and thus hides the gradients of hue and brightness in the image (Proulx and Parrott, 2008). Hence, in the canopy layer of partial-cuts, the patterns do not only appear regular because of the large uniform white areas of sky, but also because all of the objects in the picture tend to appear uniformly black (see Figure 3.3.d). On the other hand, mature and secondary forests generally have closer canopies that allow a filtering of light, thus creating gradients of brightness values. Moreover, even when canopy gaps

occur in mature and secondary forests they tend to be individually smaller and more heterogeneously distributed in the canopy thus creating more complex patterns.

3.5.3 Effects of canopy opening on the complexity of patterns among vegetation layers

The opening of the canopy by itself has a strong effect on the complexity of patterns in the different forest treatments. In the lower vegetation layers (understorey and mid forest), the complexity of patterns increases with the opening of the canopy, indicating that the diversity of spatial association between objects increases as the effects of disturbances become more severe (Figure 3.7.b, e and f). In the canopy however, the complexity of both hue and brightness patterns drops significantly below 55% canopy cover (Figure 3.7.a and b). This indicates that the same intermediate disturbance (gaps created by partial cutting) does not affect the complexity of patterns consistently from the top to the bottom of the canopy. This variation can be explained since the reduction of canopy cover in the canopy layer reveals only the underlying uniform sky patterns (Figure 3.3.d) whereas in the lowest layers the harvest of foreground trees will always reveal more background elements, thus maintaining a high diversity of object associations. However, with an ever-increasing canopy opening, it is likely that the amount of sky in the background will finally increase and cause a simplification of the patterns (and thus a decrease in MIG values) in the lower layers. Hence, we expect that a sample of forest treatments including a larger representation of forests with open canopies would present a convex relationship between canopy openness and MIG even in the lower vegetation layers.

Further study of our MIG index should also take the shape and distribution of canopy gaps into account as well as their origin (natural or anthropogenic). This will allow verification of how the variations in MIG values respond to the shape of gaps and ultimately if the maximum values of complexity that we observed always occur for the same canopy closure regardless of the origins of the gaps.

3.5.4 Complex patterns: signs of creative reorganization and resilience and confirmation of the intermediate disturbance hypothesis?

According to our work, and in accordance with the intermediate disturbance hypothesis (Connell, 1978 ; Denslow, 1985), the complexity of patterns in partial-cuts and in stands with some level of disturbed canopies is higher than in closed-undisturbed forests (Figure 3.7). As they increase the complexity of patterns, partial-cuts can thus be considered to be disturbances that encourage a "creative" reorganisation in several forest layers, which might thus increase forest resilience (Holling, 2004 ; Drever *et al.*, 2006). Partial-cuts could help recreate the conditions found in old-growth forests when natural gap dynamics help create new opportunities for stands to increase both structural and compositional diversity.

However, in this study we did not investigate the complexity of patterns found in old-growth forests since our oldest forests, the mature forests, were less than 100 year-old. It is therefore possible that old-growth forests would show more complex patterns for similar canopy opening than partial-cuts as natural gaps tend to be more heterogeneous in shape, sizes and spatial distribution. It could, for example, be hypothesised that the decrease in the complexity of patterns in forests with high canopy opening will be more rapid in anthropogenically created openings as they will consist of more contiguous and regularly shaped gaps. In addition, the forest objects in the backgrounds of the photographs that allow original spatial associations in our samples would typically be absent if the cut strips were wider or if the cutting intensity was higher, thus causing simplified patterns.

In consequence, in order to maximise the complexity of patterns, partial-cuts could be designed in order to avoid large continuous linear open areas. Similarly, the use of linear skid trails (vs. e.g. zig-zag patterns) could be questioned as they create long continuous clear-cut areas (Beaudet, Messier and Leduc, 2004).

Also, as canopy openness is particularly important for the resulting complexity of patterns (Aakala *et al.*, 2012), specific care should be given to the complexity of the

forest canopy before assigning a specific harvest method or intensity of cut. Moreover, at the scale of the entire forest (e.g. on aerial photographs), measures of the MIG of partial-cuts such as those that were studied in our work would be expected to identify relatively regular strip-cut patterns. It may therefore be advisable to not apply the same method of cutting everywhere so as to increase the overall complexity of patterns at the forest scale.

Further work including testing the complexity of patterns in more intense disturbances and older forests undergoing gap dynamics as well as at larger forest scales on aerial photographs could help confirm our findings and hypotheses.

3.6 Conclusion

Using an integrative method to measure the complexity of patterns in forests, we showed that moderate anthropogenic disturbances such as partial cutting could increase the complexity of forest patterns as measured by digital photos and as such that the intermediate disturbance hypothesis could be applied to the observation of complexity.

Most interestingly, we tested a new index to measure the complexity of forest patterns in digital forests. The use of the MIG and digital photographs accounts for the patterns created by forest objects and light in the forest. To our knowledge, this method is the only one that permits the integration of emerging patterns of light penetration into forests as a single index. Although this index could be further adjusted and tested to facilitate its interpretation, its efficiency for the evaluation of the effects of disturbances is promising.

CONCLUSION

4.1 Introduire la complexité en écologie grâce à l'étude des patrons spatiaux

L'objet de ce travail de thèse a été d'offrir un aperçu de la notion de complexité en écologie forestière. Les différents domaines qui étudient la notion de complexité ont produit, au cours des dernières décennies, de nombreuses théories et proposition de méthodes qui ont permis d'aborder des systèmes réputés imprévisibles. L'un des premiers sujets de l'étude de la complexité est d'ailleurs l'identification des sources d'imprédictibilité qui peuvent émerger par exemple, par l'action de multiples agents indépendants (météorologie, finance) (May, Levin and Sugihara, 2008) ou du fait de l'influence des conditions initiales et de l'histoire qui sont de surcroît impossibles à reconstituer intégralement et donc à intégrer dans les prévisions (sociologie, linguistique, évolution, sémiologie) (Chomsky, 1957 ; Heylighen, 1996 ; Banos, 2010 ; Solé *et al.*, 2010). Cependant, avant même d'aborder la compréhension de ses sources, la première mention de la complexité au sein d'un système vient de sa description. Souvent, les systèmes complexes (qui sont caractérisés par la multiplicité des agents influençant leurs dynamiques) ne peuvent pas être décrits par la somme de leurs composants, à moins que celle-ci soit parfaitement exhaustive. Ainsi, puisque deux systèmes différentiés par d'infimes variations peuvent suivre des dynamiques divergentes (qui mèneront d'ailleurs éventuellement à leur différentiation) seule la description de ces infimes variations au moment initial de leur comparaison peut réellement permettre la prédiction de leurs dynamiques (Stone and Ezrati, 1996). Sans pour autant être inutile à la description des systèmes, la description de leurs composants s'avère donc incomplète pour la compréhension des systèmes complexes.

La description des patrons qui émergent des systèmes complexes en revanche peut apporter une information pertinente pour la compréhension des dynamiques qui ont eu lieu puisqu'ils sont à la fois les résultats de ces dynamiques mais aussi les déterminants des interactions qui influenceront les systèmes par la suite. Ainsi, par exemple, les coupes partielles permettent de complexifier les patrons spatiaux dans les forêts mixtes (chapitre 3). Ces associations originales entre objets devraient permettre l'émergence de nouveaux processus d'interactions, notamment de facilitation indirecte pour la régénération des espèces de forêts fermées. De plus, l'apport de méthodes d'échantillonnage (photos, LIDAR) basées sur des représentations abstraites (assemblages de pixels ou de points) des objets (arbres, souches, arbuste) permettent d'extraire les patrons spatiaux indépendamment de l'identité des objets qui les composent. Cette indépendance permettant ainsi de comparer des patrons issus de compositions différentes et des systèmes différents.

La nécessité et l'efficience de cette séparation entre patrons et composition sont d'ailleurs démontrées par les résultats présentés au chapitre 2. La comparaison entre les indicateurs basés sur l'inventaire des objets et structures forestières et nos résultats de MIG (mean information gain) montre ainsi une corrélation négative entre la diversité des espèces et des structures (classes de taille des arbres, distribution de la canopée, composition du sous-bois...). La diversité spécifique et structurelle (donc probablement aussi fonctionnelle) tend finalement à uniformiser les patrons de distribution des objets en comblant tous les compartiments disponibles. Ce phénomène pourrait être comparé à une certaine saturation structurelle reflétant la complémentarité spatiale des structures végétales dans les habitats forestiers (Peterson, Allen and Holling, 1998 ; Loreau, 2004 ; Paquette and Messier, 2010).

En addition, la méthode que nous exploitons dans le chapitre 3 de ce travail nous a permis de comparer la complexité de patrons émergents d'histoires d'aménagement différentes. Nos résultats montrent non seulement que le MIG tel que nous l'utilisons permet de distinguer les effets des perturbations récentes sur des peuplements. Ces

résultats nous permettent également de conclure que 'l'hypothèse de la perturbation intermédiaire' ('Intermediate disturbance hypothesis' : IDH) (Connell, 1971 ; Denslow, 1985), qui propose que la diversité spécifique augmente du fait de l'influence de perturbations modérée, est également valable pour la de complexité des patrons de distributions. Ainsi, nous avons montré que les coupes partielles appliquées aux forêts dans le cadre de l'aménagement écosystémique ont effectivement comme effet de permettre une réorganisation des objets forestiers et d'augmenter la complexité des patrons.

Au-delà d'une indication de la complexité du système, l'étude des patrons de distribution au sein des forêts peut également apporter de l'information sur les processus qui ont eu lieu dans les systèmes (McArthur, 1972 ; Turner, 1989). En réalité, l'écologie a depuis toujours été basée sur l'interprétation des patrons spatiaux. La distribution des individus et la présence de certaines espèces indiquant à la fois les conditions environnementales qui rendent leur croissance possible, mais aussi leur capacités de dispersion ou les interactions qui influencent leur fitness (Tewksbury and Lloyd, 2001). Ainsi, les distances qui séparent différents individus, différentes espèces ou différentes communautés sont implicitement utilisées pour inférer les processus menant à la différentiation des systèmes ou à l'apparition de nouvelles espèces (Husband and Barrett, 1996). La justification de l'utilisation des patrons spatiaux en écologie est implicitement reliée au fait que les interactions entre les objets constituant les systèmes écologiques (arbres, communautés, fragments de forêt, sites de nutrition ou de reproduction...) sont directement limitées par la distance entre ces objets. Par exemple, deux arbres ne seront en compétition directe pour la lumière que s'ils sont assez proches pour se faire de l'ombre ; la distance en question étant dépendante non seulement du processus, mais aussi de l'identité (espèce et dimensions) de chacun des deux arbres (Boivin *et al.*, 2010). Cependant, différentes recherches ont également montré que les interactions indirectes pouvaient se propager le long d'un réseau d'individus et de structures, jusqu'à influencer la distribution

d'individus ou l'organisation de systèmes à distance (Wiegand *et al.*, 2007 ; Vepakomma, Kneeshaw and St-Onge, 2010). Plusieurs travaux se son récemment penchés sur les méthodes disponibles pour représenter (Chamberlin, 2009 ; Ings *et al.*, 2009) ces réseaux d'interactions les interpréter (Montoya, Pimm and Solé, 2006 ; Rayfield, Fortin and Fall, 2011) et les utiliser dans le cadre de la gestion des écosystèmes (Solé and Montoya, 2001 ; Berlow *et al.*, 2004 ; James *et al.*, 2005). En intégrant les réseaux et la théorie des graphes en écologie, ces travaux contribuent fortement à l'intégration du point de vue de la complexité en écologie. Dans le chapitre 1, nous avons montré, en dressant une revue des propriétés les plus évidentes des réseaux, que le principe des réseaux d'interactions pourrait être fonctionnel dans les systèmes forestiers même au-delà des problématiques de fragmentation. L'utilisation de structures composites (trouées, amas de bois mort, bouquets d'arbres, arbres dominants) comme 'node' dans les représentations de réseaux forestiers permettent enfin de faciliter la représentation des réseaux forestiers en se basant sur l'interprétation des patrons spatiaux.

4.2 L'utilisation des structures, objets composites et patrons abstraits en écologie

Comme illustré au travers de cette thèse, les structures ou objets composites (trouées, amas de bois mort, arbres dominants) et les patrons 'abstraits' détachés de l'identité des objets (photos, LIDAR, images satellites) sont de plus en plus fréquemment utilisés en écologie forestières. Le développement des méthodes de mesure à distance (photo aérienne, LIDAR) qui ne permettent souvent pas d'identifier les espèces ou les limites entre individus, a poussé le développement de méthodes d'interprétation ne reposant pas sur ces définitions. Dans le cadre des photos aériennes comme du LIDAR, la définition des objets dépend maintenant des limitations d'échantillonnage (densité de points, résolution) et de critères basés sur les différences de représentations entre objets plutôt que sur la définition des individus en

eux même. Ainsi, par exemple, dans une représentation au LIDAR de la canopée, les trouées sont définies par leur différence de hauteur par rapport à leur entourage, et non pas par la présence d'un chablis ou l'ouverture vers le ciel. Ces représentations sont évidemment calibrées de manière à se rapprocher de la réalité telle que définie par les méthodes traditionnelles d'échantillonnage, et finissent par rapporter des résultats très analogues (Vepakomma, St-Onge and Kneeshaw, 2008 ; Vierling *et al.*, 2008). Ces méthodes en plus de permettre des échantillonnages sur des larges surfaces ont également contribué à détacher la fonction des objets dans le système de leur espèce ou de leurs dimensions individuelles, et de l'attribuer plutôt au voisinage d'objets formant le patron. Ainsi, l'espèce et la taille de l'arbre ayant formé le chablis ont perdu de leur importance dans la caractérisation de la trouée, pour la céder aux dimensions de la trouée en elle-même et au potentiel de cette trouée à 'rompre' le patron environnant. De ce point de vue, la notion de 'structure clef de voûte' ('keystone structure') (Tews *et al.*, 2004 ; Manning, Fischer and Lindenmayer, 2006) dont l'importance pour le système se distingue non seulement par son identité (type, dimension) mais surtout par sa rareté le pourrait être réellement utilisée grâce à ces méthodes d'échantillonnage. En amenant l'attention des chercheurs vers des assemblages de traits complémentaires plutôt que sur des inventaires d'espèces l'écologie fonctionnelle a également contribué à cet intérêt renouvelé pour les structures en tant que support de fonctions pour l'écosystème et non plus comme assemblage d'individus à inventorier. Dans ce contexte, les travaux que nous avons menés dans cette thèse sur le MIG (chapitres 2 et 3) constituent eux aussi une proposition d'approche des patrons d'une manière plus intégrative. En passant par la photographie numérique, les assemblages spatiaux entre objets individuels sont décrits directement et analysés par le MIG strictement du point de vue du patron qu'ils forment. Les variations de complexité de ces patrons dans les forêts permettant ainsi de refléter la variabilité du système dans son ensemble. Par exemples, nos résultats du chapitre 2 montrent que la complexité des forêts coupées à 35% est beaucoup plus variable que celle des forêts matures. Ce résultat indique non

seulement que les coupes ont pour effet d'augmenter la complexité, mais également que cette complexité est hétérogène dans le peuplement, reflétant ainsi le design des coupes par bandes. Ainsi des conclusions issues de l'étude de patrons relativement éloignés des objets concrets (arbres, plantes du sous-bois et même trouées) peuvent apporter des informations propres à être utilisées pour la compréhension des relations entre sous-ensembles du système et pour l'aménagement.

4.3 Introduire la complexité en aménagement : principes généraux pour un changement d'approche

L'introduction du point de vue de la complexité en aménagement forestier apporte de nouveaux outils pour le suivi des systèmes, mais nécessite également une remise en cause de certains paradigmes de gestion (Messier and Kneeshaw, 1999 ; Drever *et al.*, 2006). S'il devait être admis que les forêts doivent être gérées comme des systèmes complexes, l'imprédictibilité intrinsèque de ces systèmes devrait également être intégrée dans les processus de décision (Messier and Puettmann, 2011). Le travail de gestion forestière devrait alors engager une transition depuis une approche de consommation des ressources vers une gestion de l'imprédictibilité des systèmes. Une gestion basée sur la gestion de l'imprédictibilité ne consiste pas uniquement à ménager des enveloppes d'incertitude autour des prédictions (Puettmann, Coates and Messier, 2009). Ces enveloppes doivent également être resserrées lorsque l'imprédictibilité du système devient trop importante. Ces resserrements peuvent être appliqués dans l'espace, en identifiant des composants des systèmes qui sont naturellement linéaires ou qui sont suffisamment importants pour qu'il soit rentable de les manipuler activement et ainsi garantir leur dynamique. Le resserrement des incertitudes doit aussi avoir lieu dans le temps en fonction des dynamiques, soit en contrôlant l'état du système pour réviser le modèle (Lindenmayer, Franklin and Fischer, 2006) et éventuellement en intervenant pour 'redresser' la dynamique dans l'espoir de la ramener vers la trajectoire prévue.

Cette approche consisterait dans un premier temps à identifier les éléments qui influencent fortement la dynamique des systèmes forestiers et qui peuvent par conséquent influencer considérablement leur prévisibilité. La méthode que nous présentons dans le chapitre 1 et qui est basée sur la représentation des réseaux d'interactions dans les peuplements constitue en fait un premier pas vers la caractérisation des objets forestiers qui peuvent être des sources de variabilité importante pour la dynamique des systèmes. L'identification de ces 'hubs' dans les systèmes forestiers fragmentés permet par exemple une gestion plus intégrée de la distribution spatiale des unités d'exploitation et des réserves (James *et al.*, 2005).

D'autre part, et à plus petite échelle, l'identification des 'nodes' importants au sein des différentes communautés qui composent la forêt, permettrait d'envisager une adaptations des modes de récolte en fonction des structures qui favorisent la conservation des espèces ou la construction de patrons spatiaux favorables à la faune (Tews *et al.*, 2004). L'étude des réseaux d'interactions entre les objets forestiers pourrait aussi éventuellement permettre de définir les échelles auxquelles les systèmes et sous-systèmes sont organisés, par exemple en identifiant les 'clusters' d'objets constituant des sous-systèmes presque indépendant (Rayfield, Fortin and Fall, 2011). De cette manière, l'imprédictibilité des dynamiques de restauration et de perturbation pourraient être définie pour chaque sous-système, et les trajectoires susceptibles de propager cette imprédictibilité dans l'ensemble de la forêt pourraient être contrôlés.

En conclusion, la transition de la gestion forestière vers une gestion des forêts complexes repose principalement sur une adaptabilité active aux dynamiques des systèmes et donc sur la connaissance des dynamiques forestières et des patrons spatiaux qui les révèlent.

4.4 Future recherche

Les champs de recherche ouverts dans le cadre des systèmes écologiques complexes sont innombrables. Cependant, considérant les résultats de notre travail, certains sujets nous paraissent tout particulièrement intéressants.

Tout d'abord, et suivant la proposition d'adapter la théorie des réseaux pour l'aménagement forestier, un ensemble de recherches sur les différentes étapes de l'application de cette idée est nécessaire. Les différents indices permettant de définir les échelles de discontinuités des systèmes ainsi que les éléments structurels remarquables ('hubs', 'bottlenecks', 'clusters'...) devraient être testés sur le terrain dans le cadre d'un projet à grand échelle. L'utilisation de parcelles permanentes où tous les objets forestiers sont cartographiés à l'échelle du peuplement pourrait faciliter cette étude en fournissant les données nécessaires à l'application des différents indices spatiaux et permettrait de surcroît l'observation de la variation de la structure des réseaux dans le temps. Mais ce genre d'information obtenu au niveau du peuplement devrait aussi être relié à l'échelle du paysage afin de rendre l'information applicable à un territoire forestier donné.

Un deuxième axe de recherche complémentaire se situe dans l'utilisation des patrons spatiaux et temporaux et de leur complexité pour la caractérisation et le suivi des systèmes forestiers. Plusieurs indices peuvent être utilisés, et notamment le MIG, mais ils nécessitent encore d'être validés et étudiés dans différents contextes écologiques afin de mieux faire ressortir leur utilité potentiel. . Notamment, ce type d'indice devrait être étudié les effets des perturbations sur la complexité des patrons en fonction de la diversité spécifique et fonctionnelle. Il est en effet possible que la diversité spécifique, et surtout la manière dont cette diversité s'exprime en termes de diversité fonctionnelle (complémentarité ou redondance), affecte les résultats d'indices basés sur la représentation visuelle des patrons spatiaux. De plus, certains systèmes extrêmes en termes de diversité structurelle et spécifiques comme les

plantations et les forêts tropicales pourraient être intégrés à la comparaison afin de mieux cerner les limites d'applicabilité de cette méthode.

Enfin, considérant l'importance des patrons de lumière dans nos résultats, une approche de l'évaluation des méthodes de coupes basées sur un indicateur représentant la distribution spatiale de la lumière et son interaction avec les objets forestiers devrait être développée. Une telle approche pourrait être basée sur la photographie numérique, qui intègre les effets des objets sur la lumière ou sur des mesures de lumière répétées dans l'espace. La complexité de tels patrons de lumière pourrait servir de base pour une nouvelle approche de la représentation des structures en forêt.

L'étude de la complexité n'en est qu'à ses débuts en forêt, et le potentiel de cette approche pour l'étude de nombreux domaines (biologie, économie, sociologie...) n'est plus à démontrer. Ces domaines restent une large source d'inspiration pour l'incorporation de la complexité à l'étude des forêts.

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